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METAPODIAL RESTRUCTURING IN *MAMMUT* AND
RECENT ELEPHANTS: EVIDENCE OF DISEASE OR
PHYSICAL STRESS?

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METAPODIAL RESTRUCTURING IN *MAMMUT* AND RECENT ELEPHANTS: EVIDENCE OF DISEASE OR PHYSICAL STRESS?

By

Kathlyn Mai Smith

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ABSTRACT

METAPODIAL RESTRUCTURING IN *MAMMUT* AND RECENT ELEPHANTS: EVIDENCE OF DISEASE OR PHYSICAL STRESS?

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A variety of pathologies have been noted on *Mammut americanum* (American mastodon), including subchondral articular surface undermining on metapodials (documented in extinct bison). Metapodial undermining in mastodons has been ascribed to tuberculosis (*Mycobacterium tuberculosis*), but this diagnosis has not been tested by comparisons with Recent material. The following questions are here addressed by comparisons with Recent proboscideans: (1) To what degree do Recent elephants show undermining? (2) Does undermining vary based on species, age, sex, or whether the animal is wild or captive? (3) Does undermining preferentially affect a specific metapodial? and (4) Can this undermining be firmly linked to tuberculosis in Recent elephants, and be used to interpret the presence of the disease in the American mastodon?

To answer these questions, 165 metapodials from 17 skeletal specimens of Recent elephants were examined for the presence of undermining. Of the 165 metapodials studied, 103 (62%) had undermining. The third metapodial most often had undermining (31 of 35; 89%). Undermining differentially affected adult elephants; no juvenile elephants in the study had undermining. Because undermining in Recent elephants affected only adults, and was most often present on the central metapodials, it is likely the result of pressure on the feet from the weight of the animal, and a normal part of Recent proboscidean skeletal anatomy, rather than the result of an infection.

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KEY TO ABBREVIATIONS

L-CAL	left calcaneum
R/L-MPI (II,III,IV,V)	right or left metapodial one (two, three, four, five)
R/L-MCI (II,III,IV,V)	right or left metacarpal one (two, three, four, five)
R/L-MTI (II,III,IV,V)	right or left metatarsal one (two, three, four, five)
RM/LM-PPI (II,III,IV,V)	first proximal phalanx of the right or left manus (second, third, fourth, fifth)
RP/LP-PPI (II,III,IV,V)	first proximal phalanx of the right or left pes (second, third, fourth, fifth)
LM-IPI (II,III,IV,V)	intermediate phalanx of the left manus (second, third, fourth, fifth)

INTRODUCTION

One of the most notable members of North America's Pleistocene fauna is *Mammut americanum*, the American mastodon. Mastodons are found throughout the continent, but are concentrated in the Great Lakes region (King and Saunders, 1984; Tassy and Shoshani, 1988; Holman, 1995); in Michigan alone mastodon fossils have been recovered from over 250 locations across the state (Abraczinskas, 1993), leading Michigan to adopt it as the state fossil in 2002.

Paleopathological analyses of mastodons indicate that they suffered from a variety of diseases and injuries (Bricknell, 1987; Fisher, 1984; Rothschild et al., 1994; Rothschild and Helbling, 2001). Pathologies, and non-pathological injuries, attributed to mastodon skeletal elements include arthritis, butchering scars, periodontal disease, and, most recently, tuberculosis. Tuberculosis, as caused by the microbiologic agent *Mycobacterium tuberculosis*, has, in addition to mastodons, been identified in humans, extinct bison, captive elephants, and in pets and other captive animals in contact with humans (Rothschild et al., 2001; Hoop, 2002; Lomme et al., 1976; Powers and Price, 1967). Rothschild and Helbling (2001) identified tuberculosis in the fossil record on the basis of subchondral articular surface undermining in metapodials (Rothschild and Helbling, 2001), but this has not yet been tested by comparison with Recent material.

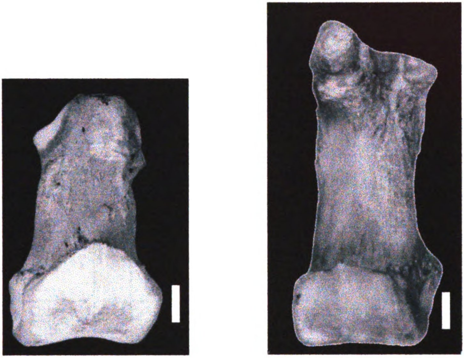
Despite splitting into separate phyletic lineages 20 million years ago (Tassy, 1996), mastodons and elephants retain similar body plans and skeletal anatomy. The proboscidean skeleton is constructed as a graviportal support system. Adaptations for this body type include columnar limbs, a light skull with a large surface area for muscle attachment, the replacement of a bone marrow cavity with a network of dense, cancellous

bone, and mesaxonic limbs (Shoshani, 1996, and references therein). The difference between mastodon and elephant feet is that mastodons have stockier foot bones, while elephants generally have more slender foot bones (Figure 1). In metapodials, the elements focused on in this study, the ratio of height:length is generally less in mastodons than it is in elephants. The number of digits, stance, and general shape of the foot bones for both groups of proboscideans remain the same.

The objective of this research is to evaluate subchondral articular surface undermining in mastodon metapodials by comparison with the skeletal anatomy of Recent proboscideans. The following questions will be addressed: (1) To what degree do Recent elephants show the undermining? (2) Does the undermining vary based on species, age, sex, or whether the animals are wild or captive? (3) Does articular surface undermining preferentially affect a specific metapodial? and (4) Can this undermining be firmly linked to tuberculosis in Recent elephants, and thus be used to interpret the presence of the disease in fossil proboscideans, including the American mastodon?

The Order Proboscidea

Proboscideans are fairly well-represented in the fossil record (Figure 2). Shoshani and Tassy (1996) recognized 8 to 9 families (depending on the inclusion or exclusion of *Anthracobune*, tentatively considered the oldest Proboscidean), 38 genera, and 162 species. The Order Proboscidea is traditionally accepted to have first appeared in Africa during the Early Eocene with the extinct genus *Moeritherium* (Fischer and Tassy, 1993; Thewissen and Domning, 1992; Tassy, 1996). Fossil material of *Moeritherium* shows that it had a variety of proboscidean characteristics, including: the loss of the lower



A **B**

Figure 1. The L-MTIII of MSUVP 1289 (A), an American mastodon, and the L-MTIII of USNM 163318 (B), an African elephant. Note that the mastodon is stouter, and has a wider distal articular surface. Both metatarsals show articular surface undermining. Scale bar = 2 cm.

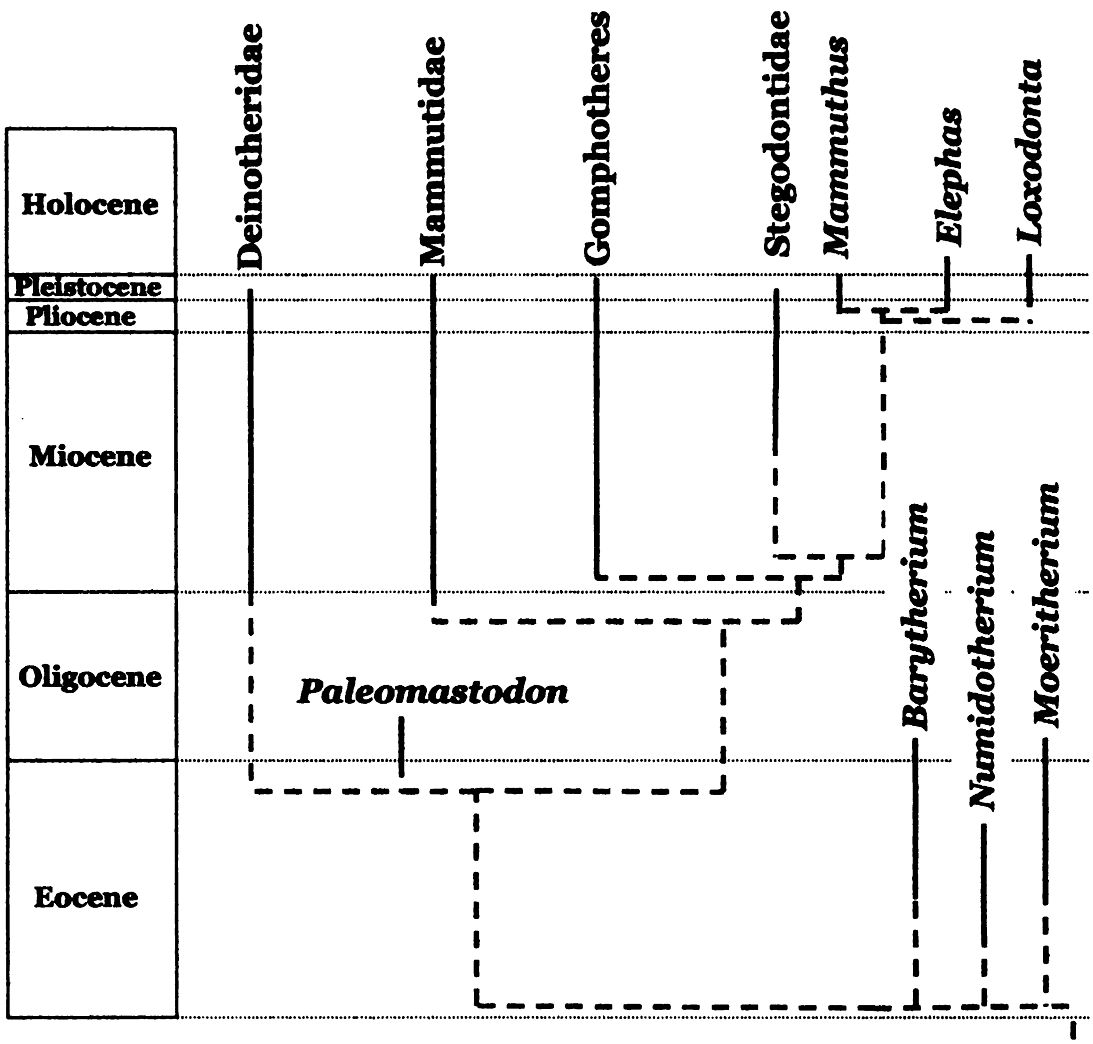


Figure 2. The phylogenetic relationships within Order Proboscidea. Adapted from Shoshani and Tassy (1996) and Thomas et al. (2000)

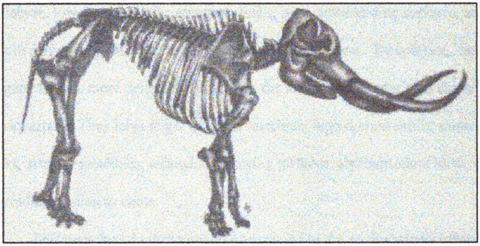
incisor, the loss of the lower canine, the loss of the upper and lower first pre-molar, greatly enlarged, tusk-like second upper and lower incisors, the flattening of the femur, the absence of a saggital crest, and the absence of pneumatization in the crania, among other characters as noted by Tassy (1996), based in part on work by Andrews (1906).

The Superfamily Elephantoidea includes the families Mammutidae, Gomphotheridae, Stegodontidae, and Elephantidae. This group shows tooth displacement (Tassy and Shoshani, 1988), in which the cheek teeth erupt behind teeth already in use, and push forward until they become functional; they eventually are replaced themselves and resorbed at the anterior end of dentition. This displacement continues until the third molars are the only teeth present at the end of the full sequence.

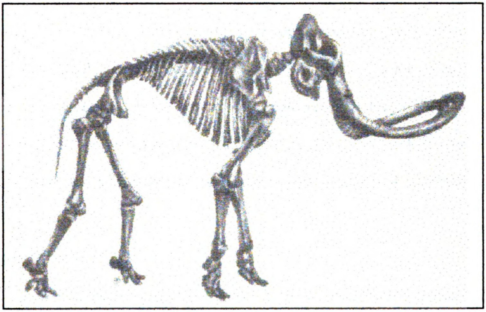
This study focuses on the families Mammutidae and Elephantidae. Mammutidae emerged in Africa during the Early to Middle Miocene; characteristics of the family include a broad, low cranium, a shortened mandible, and a laterally compressed rostrum. The group reached North America by the late Pliocene with *Mammut*, the first genus to develop subhypsodont cheek teeth (Saunders, 1996).

The Family Elephantidae first appeared in the Late Miocene of Africa (Thomas et al., 2000). Prior to Elephantidae, proboscideans chewed in a grinding and shearing motion; this shifted to horizontal shearing with a fore and aft movement of the jaw in elephantids (Maglio, 1972). Elephantidae includes the iconic Ice Age form, the mammoth (*Mammuthus*), and the two genera of Recent elephants, *Loxodonta* and *Elephas*.

There are numerous skeletal differences between mammoths and mastodons. As described by Shoshani (1992), mastodons (Figure 3A) have stockier, heavier bodies; the



A. American mastodon (*Mammut americanum*).



B. Jefferson mammoth (*Mammuthus jeffersoni*).

Figure 3. Skeletal differences between (A) mastodons and (B) mammoths. From Skeels (1962).

head and shoulder is only slightly above the hindquarters. They have 20-21 thoracic vertebrae, low-domed skulls, straighter tusks, bunodont chewing surfaces, and brachyodont teeth, and they use a grinding surface to chew. By contrast, mammoths (Figure 3B) are more delicately built, with the head and shoulder well above their hindquarters. They have fewer thoracic vertebrae, high-domed skulls, more curvaceous tusks, shorter mandibles, lophodont chewing surfaces, and hypsodont teeth, and they use a grinding motion to chew.

Different dental morphologies correspond to the environments inhabited by each taxon. Palynological evidence collected in Michigan for the interstadial intervals of the Wisconsinan glaciation indicate that the environment was boreal forest or forest tundra (Holman et al., 1986). This environment was perfect for mastodons, with over 250 specimens found in the state to date (Abraczinskas, 1993). The mastodon adapted well to a range of habitats, and has been termed an ecological generalist. On the contrary, the mammoth was an ecological specialist (Shoshani, 1989), and was better adapted to live in grasslands and treeless tundra-steppe areas (Agenbroad and Mead, 1996).

Extant Proboscideans

The two surviving genera of Proboscidea are found in areas throughout Africa and Asia (Figures 4 and 5). There are two subspecies of African elephants (*Loxodonta africana africana* and *Loxodonta africana cyclotis*) and three subspecies of Asian elephants (*Elephas maximus maximus*, *Elephas maximus indicus*, and *Elephas maximus sumatranus*).

L. a. africana is commonly referred to as the savanna elephant. It is the

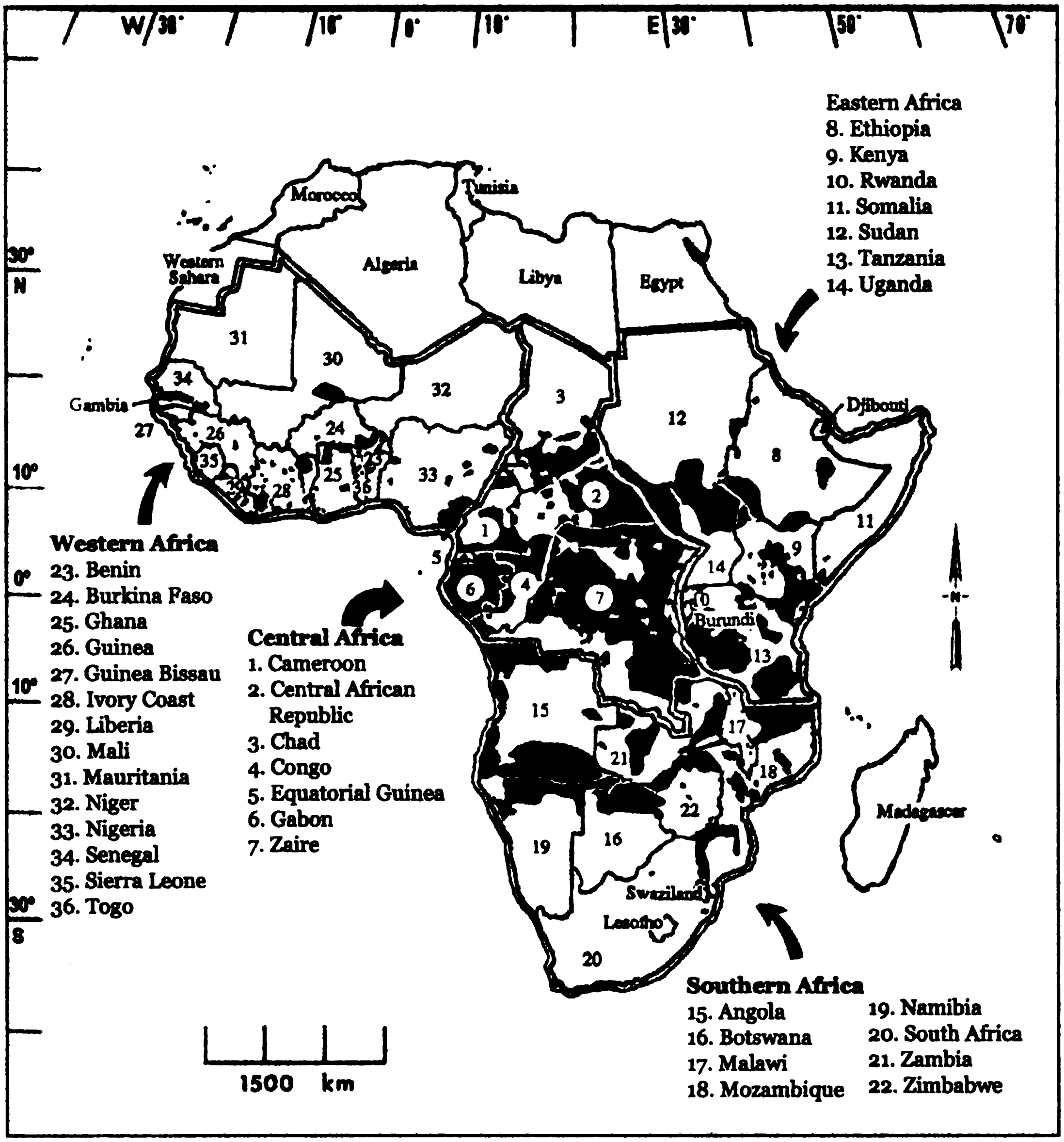


Figure 4. The present distribution of African elephants (*Loxodonta africana*). From Douglas-Hamilton and Michelmore (1996)

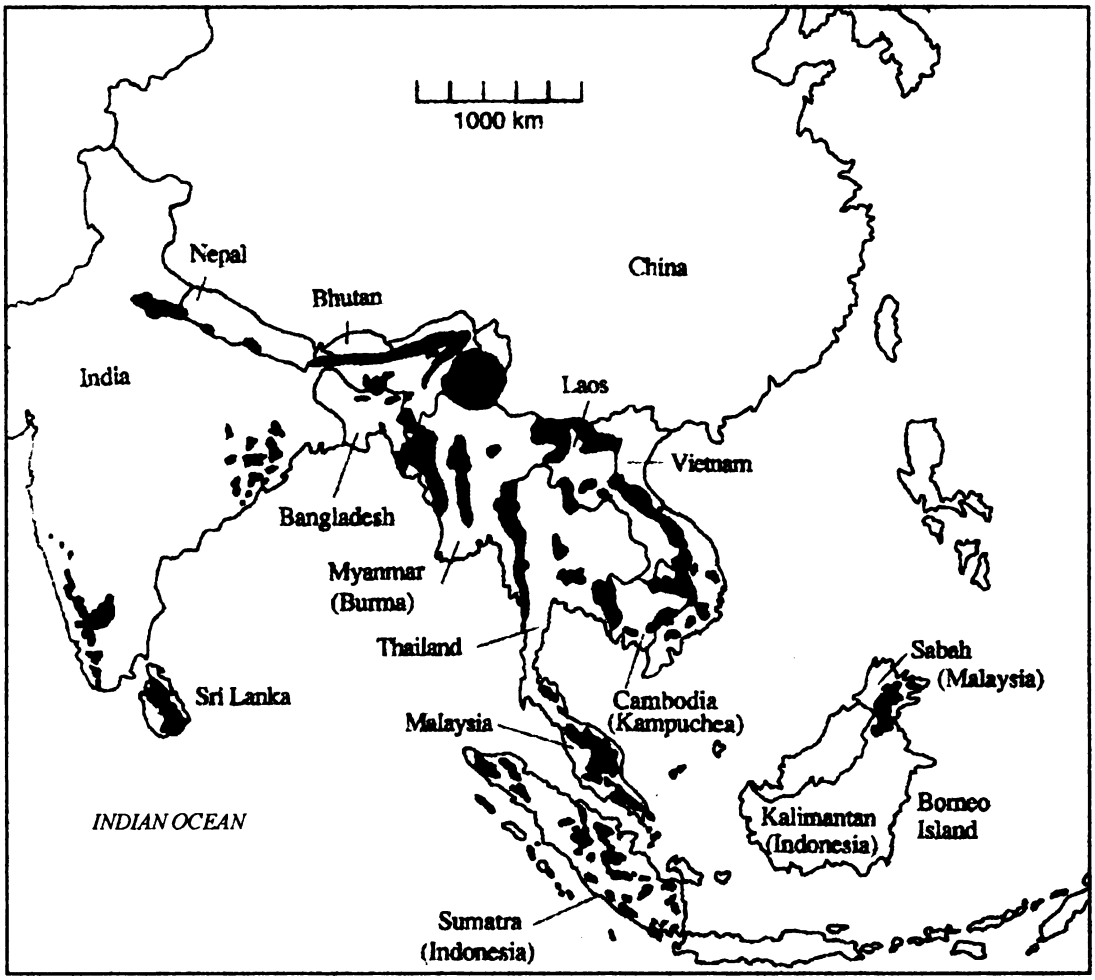


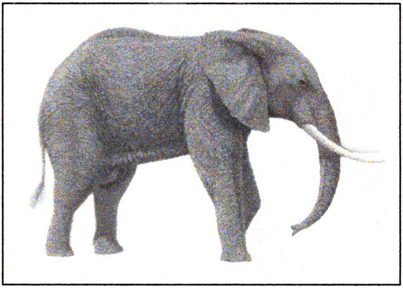
Figure 5. The present distribution of Asian elephants (*Elephas maximus)* elephants. From Sukumar and Santiapillai (1996).

largest living land animal, weighing between 8800 and 15,400 pounds, and standing between 9.8 and 13 feet tall (Shoshani, 1992). It has dark skin, hair around the trunk and mouth, triangular ears, and curved, thick tusks (Figure 6A). The forefeet have 4 toenails, and the hind feet have 3 toenails (Ramsay and Henry, 2001). The savanna elephant lives in various habitats in Africa, south of the Sahara desert, including open grasslands, forests, deserts, marshes, and lake shores.

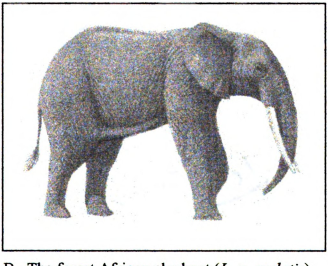
L. a. cyclotis is commonly referred to as the forest elephant. As noted by Shoshani (1992), it is smaller than the savanna elephant, weighing between 4400 and 9900 pounds, and standing between 6.6 and 9.8 feet tall. It is lighter in color and has less hair; its ears are rounder and smaller, and its tusks are straighter and more slender (Figure 6B). The forefeet have 5 toenails, and the hind feet have 4 toenails (Ramsay and Henry, 2001). The forest elephant lives mainly in equatorial forested regions in central and western Africa, as well as in intermediate zones between forests and grasslands.

E. m. maximus is commonly referred to as the Sri Lankan elephant. As described by Shoshani (1992), it weighs between 4400 and 12,100 pounds, and stands 6.5 to 11.5 feet tall. It is the darkest Asian elephant, with large ears, and depigmentation patches on its ears, face, trunk, and belly (Figure 7A). The forefoot has five toenails, and the hind foot has four toenails (Ramsay and Henry, 2001). This subspecies lives only on the island of Sri Lanka, and exists in a variety of habitats, including open grasslands, forests, transitional areas, open savannahs, marshes, and lake shores, from sea level to the mountains.

E. m. indicus is the mainland Asian elephant subspecies. Shoshani (1992) notes its weight between 4400 and 11,000 pounds, and height between 6.5 and 11.5 feet.

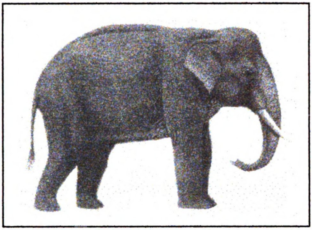


A. The savanna African elephant (*L .a. africana*).

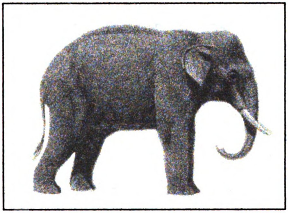


B. The forest African elephant (*L. a. cyclotis*).

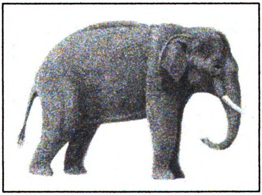
Figure 6. African elephant (*Loxodonta africana*) subspecies: (A) savanna elephant (*L. a. africana*); (B) forest elephant (*L. a. cyclotis*). From Shoshani (1992).



A. The Sri Lankan Asian elephant (*E. m. maximus*).



B. The mainland Asian elephant (*E. m. indicus*).



C. The Sumatran Asian elephant (*E. m. sumatranus*).

Figure 7. Asian elephant (*Elephas maximus*) subspecies: (A) Sri Lankan elephant (*E. m. maximus*); (B) mainland elephant (*E. m. indicus*); (C) Sumatran elephant (*E. m. sumatranus*). From Shoshani (1992).

than the Sumatran elephant; its ears are of variable size (Figure 7B). There are five toenails on the forefoot, and four toenails on the hind foot (Ramsay and Henry, 2001). This elephant lives in 12 mainland countries, from India in the west to Indonesia in the east, and prefers forested areas and transitional zones between forests and grasslands; it can live from sea level to 2000 meters.

E. m. sumatranus is the Sumatran elephant. Shoshani (1992) lists its weight as between 4400 and 8800 pounds, and height between 6.5 and 10.5 feet. It is the lightest-colored elephant , and has disproportionately large ears (Figure 7C). Unlike the other Asian subspecies, which have 19 pairs of ribs each, the Sumatran elephant has 20 pairs of ribs. It has five toenails on the forefoot, and four toe nails on the hind foot (Ramsay and Henry, 2001). The Sumatran elephant lives only on the island of Sumatra, mainly in forests and patchy habitats.

Paleopathology in proboscideans

Paleopathology is the study of ancient diseases. An individual can be affected throughout its lifetime with a variety of diseases, illnesses, and injuries. If these ailments cause bone to restructure, paleopathological interpretations can be made from skeletal remains. Pathologies, and non-pathological injuries, may show up as bony signatures, including lesions, fusings, erosions, fractures and breaks. Previous studies on skeletal elements of fossil proboscideans show that they suffered from a variety of pathologies, including osteoarthritis, spondyloarthropathy, periodontal disease, diffuse idiopathic skeletal hyperostosis, and tuberculosis (Rothschild et al., 1994; Rothschild and Helbling, 2001; Bricknell, 1987). Osteoarthritis is generally observed as a bony overgrowth on the

2001; Bricknell, 1987). Osteoarthritis is generally observed as a bony overgrowth on the zygapophyseal joints; severe arthritis may cause grooving of articular surfaces and the changing of bone into an ivory-like mass at the surface. Evidence for spondyloarthropathy includes erosions on the dorsal superior and dorsal inferior borders of the lower thoracic and lumbar vertebrae, giving the vertebral centrum a squared appearance; vertebral fusion can also be a sign of spondyloarthropathy. Periodontal disease causes a ridge and groove where the tooth and gums meet, giving the jaw a lumpy appearance. Diffuse idiopathic skeletal hyperostosis is identified by the ossification of the ligaments between vertebrae, and resembles melting wax. Tuberculosis has been identified in mastodons on the basis of a periosteal reaction on ribs, and subchondral articular surface undermining on foot bones.

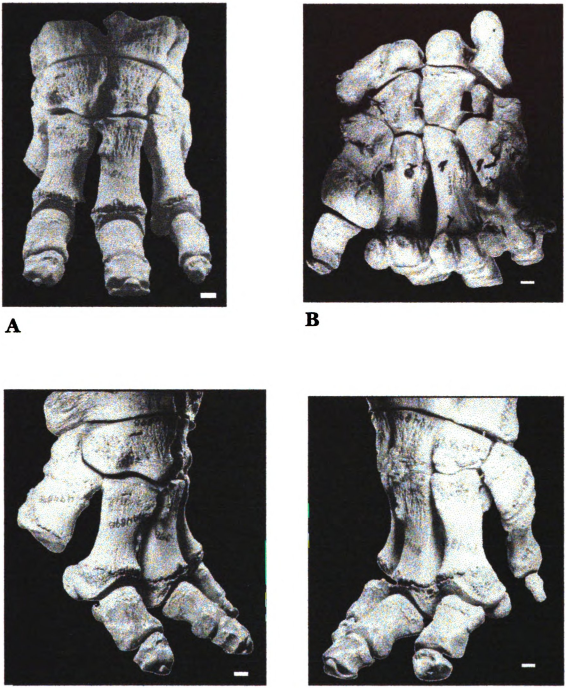
Evidence of bone restructuring, caused by disease, injury, or everyday activity, can provide information on lifestyle and habitat. For example, two Columbian mammoths (*Mammuthus columbi*) were discovered with their tusks interlocked (Shultz, 1963). The orientation of the skeletons, in conjunction with the marks on the tusks, suggests that the mammoths were engaging in battles similar to those between bull African elephants (Rothschild and Martin, 1993). Another instance of tusk use can be inferred from wear patterns. African elephants fell trees and break them with their tusks. Living elephants tend to favor one tusk or the other when performing this act, and mastodons likely did the same. When a mastodon skull is recovered with both tusks intact, the tusk on one side is typically shorter or more worn down than the other, suggesting that mastodons were either "right- or left-tusked" (Holman, 1975).

Most evidence of disease on bone has been documented on human skeletons, and

it is a challenge to identify the disease in non-human vertebrates, as a single disease can affect different vertebrates in distinctly different ways. Thus, it is important to do further testing for the diagnosis of diseases on fossil material based on physical characteristics, in order to assign bone reactions to particular diseases. Rothschild et al. (2001) performed such an analysis on the foot bones of an extinct bison. The pathologies identified on the foot bones were suggestive of tuberculosis. Fragments of DNA from the area affected by pathology were isolated and sequenced. Sequencing of these fragments identified the DNA of a member of the *M. tuberculosis* complex, confirming the association of the physical character attributed to tuberculosis with the putative infection agent.

Elephant foot skeletal anatomy

The structure and components of the feet of African and Asian elephants are similar, yet the higher frequency of foot problems in captive Asian elephants suggests an unrecognized biological difference (Ramsay and Henry, 2001). The elephant manus (Figure 8) is semi-digitigrade (Fowler, 2001); it consists of carpals, metacarpals, and phalanges. The elephant carpus comprises two block-like stacks of four bones each. The distal four carpals articulate with corresponding metacarpals I through IV, while MCV also articulates with the fourth carpal. In African elephants, the first digit has one phalanx and one sesamoid bone; in Asian elephants, the first digit has two phalanges and one sesamoid bone. Digits two, three, and four each have three phalanges; the fifth digit has two phalanges. Digits two through five each have paired sesamoid bones that articulate with the posterior distal articular surface on metacarpals two through five



A B

C D

Figure 8. The African elephant manus; USNM 49489B: (A) right manus anterior view; (B) left manus posterior view (C) right manus lateral view; (D) right manus medial view. Scale bar = 2cm.

(Ramsay and Henry, 2001).

The elephant pes (Figure 9) is smaller than the elephant manus, and semi-plantigrade (Fowler, 2001); it consists of tarsals, metatarsals, and phalanges. The tarsus comprises seven bones in three rows. Like the forefoot, the four distal tarsal bones articulate with corresponding metatarsals one through four; the fifth metatarsal articulates with the fourth tarsal as well. In Asian elephants, the first digit has one phalanx; in African elephants, the first digit has one sesamoid bone and no phalanx. All other digits have associated paired sesamoid bones located on the distal articular surface of the metatarsals, on the posterior side. In Asian elephants, the second digit has two phalanges; in African elephants, the second digit has three phalanges. In both species, digits three and four have three phalanges each, and digit five has two phalanges (Ramsay and Henry, 2001).

The smallest metacarpal is MCI, which is medially positioned, and nearly triangular in shape (Figure 10A). Moving medially to laterally, the next bone is MCII (Figure 10C), which is approximately twice as long and twice as wide as MCI. MCIII is the largest metacarpal, and centrally positioned (Figure 10E). MCIV (Figure 10G) is slightly longer and considerably wider than MCII, and shorter and wider than MCIII. MCV, which is the lateral-most metacarpal, is the most block-like bone (Figure 10I). It is slightly shorter than MCIV, and about the same width (Ramsay and Henry, 2001; Smuts and Bezuidenhout, 1993). The metatarsals follow the same size pattern, but they are smaller and stockier than their metacarpal counterparts (Figure 10).

Each metapodial widens towards its proximal and distal ends; the distal end is distinctly wider than the proximal end, except for the first metapodial, which has distal

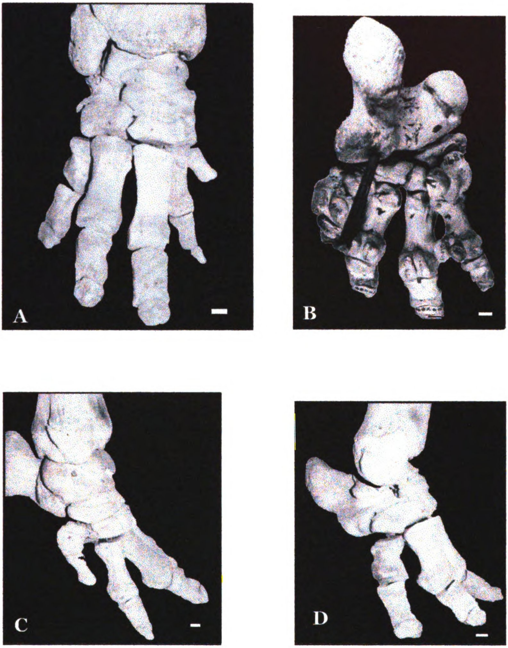


Figure 9. The African elephant pes: (A) MR.7550 right pes, anterior view; (B) USNM 49849B left pes, posterior view (R-MTI not shown); (C) MR.7550 left pes, medial view; (D) MR.7550 right pes, lateral view. Scale bar = 2 cm.

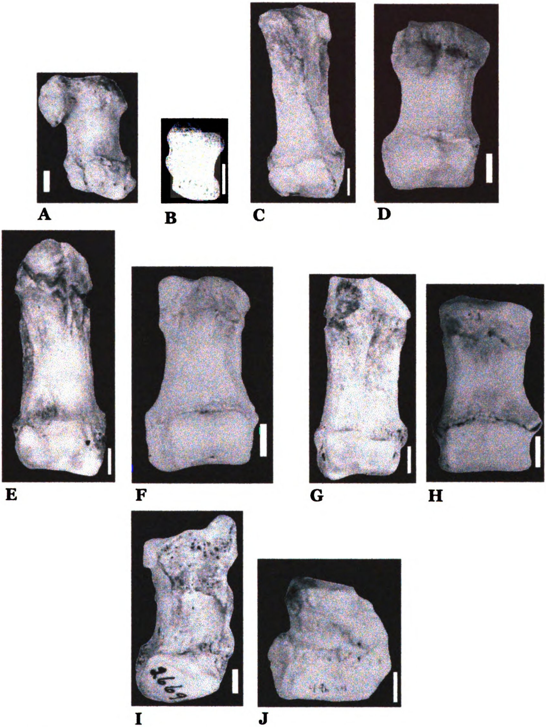


Figure 10. Elephant metapodials (posterior view). (A) USNM 266911 R-MCI; (B) USNM 49639 L-MTI; (C) USNM 266911 R-MCII; (D) USNM 49639 L-MTII; (E) USNM 266911 R-MCIII; (F) USNM 49639 R-MTIII; (G) USNM 266911 R-MCIV; (H) USNM 49639 L-MTIV; (I) USNM 266911 R-MCV; (J) USNM 49639 L-MTV. Scale bar = 2 cm.

and articular ends of about the same width. Elephant metacarpals represent typical features of metapodials in general, in that they are elongate in shape and approximately quadrilateral in cross-sectional shape (Smuts and Bezuidenhout, 1993).

There are a number of articular facets on metapodials. The first metapodial has three articular facets, one proximally to articulate with the first carpal, and two distally: one on the anterior that articulates with the first phalanx, and one on the posterior that articulates with the proximal sesamoid bone. The second metapodial has four proximal articular facets (medially for carpals one, two, and three, and laterally for MCIII), and three distally (one for PPII, and two for sesamoid bones). The third metapodial has four facets on the proximal articular surface (medially for MCII, one for the third carpal, one for the fourth carpal, and one laterally for MCIV). Distally, there is one facet for articulation with PPIII, and 2 facets for two sesamoid bones. The fourth metapodial has three articular facets proximally (one for MCIII, one for carpal IV, and one for MCV), and three distally (one for PPIV, and two for sesamoid bones). The fifth metapodial has three proximal articular facets (one for MCIV, one for carpal IV, and one for the ulnar carpal bone), and three distal facets (one for PPV, and two for sesamoid bones) (Smuts and Bezuidenhout, 1993).

This study focuses on the distal articular surfaces of the metapodials. The articular facets in questions are those that articulate with sesamoid bones, which are found on the posterior side of the metapodial (Figure 11A).

Tuberculosis

Tuberculosis is a non-pyogenic form of osteomyelitis; it inflames the bone, but is

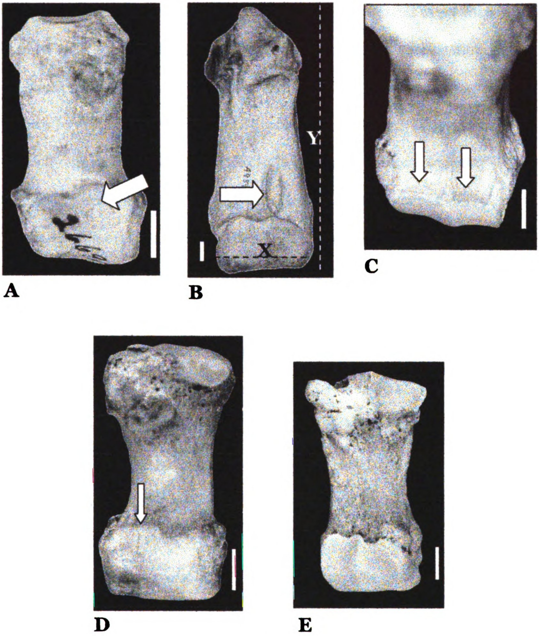


Figure 11. (A)USNM 266911 R-MTII. Arrow denotes location of distal articular surface. (B) FMNH 49894 R-MCIII: (X) location of width measurement; (Y) location of length measurement. Arrow denotes the location of posterior depression. (C) FMNH 60601 R-MTIII. The arrows denote the location of articular surface undermining. (D) USNM 266911 L-MTIV. Arrow denotes "lipping" of the articular surface. (E) USNM 588113 R-MTIV. In life, this individual was infected with tuberculosis. This bone shows articular surface undermining. Scale bar = 2 cm.

not pus-forming. It is a bacterial infection, caused by a microbiologic agent, and is transferred through air. The origin of *Mycobacterium tuberculosis* is as yet unknown. In the fossil record it is often difficult to determine which strain of mycobacterium affects the individual; the infecting agent is then termed part of the "*Mycobacterium tuberculosis* complex," which consists of *M. tuberculosis*, *M. bovis*, *M. africanum*, and *M. microti* (Frothingham et al., 1999). Extinct bison, sheep, musk ox, and other bovids have been diagnosed with skeletal lesions characterized as tubercular, caused by a member of the *M. tuberculosis* complex (Rothschild et al., 2001). Humans (Rothschild and Martin, 1993), captive Asian elephants (Mikota et al., 2000), mastodons (Rothschild and Helbling, 2001), captive oryxes (Lomme et al., 1976), pet birds (Hoop, 2002), and an isolated African elephant (Urbain, 1938) have all been reported as infected with *M. tuberculosis*. *Mycobacterium bovis* has been reported as a problem in various extant species; white-tailed deer, domestic cattle and African buffaloes are highly susceptible to infection (Michel, 2002). It has been suggested that the human tuberculosis epidemic resulted from the spread of *M. tuberculosis* complex from domesticated animals to man (Taylor et al., 1999).

Mycobacterium tuberculosis, the agent that causes infection in elephants and humans, is suggested to have an origin between 15,000 and 20,000 years before the present (Sreevatsan et al., 1997). The paleopathological character reported as pathognomonic for tuberculosis on bone, articular surface undermining on foot bones, has been noted on humans (Rothschild and Martin, 1993), as well as on extinct longhorn bison (*Bison antiquus*) (Rothschild et al., 2001), before being identified on mastodons (Rothschild and Helbling, 2001). The bison, dated at 17,870 ± 230 years before the

present, is the earliest known paleopathological evidence for the occurrence of tuberculosis in North America. Paleopathological evidence of *M. tuberculosis* was found in human remains from more than 3,700 years ago (Ayvazian, 1993), and in elephants 2,000 years ago (Mikota et al., 2000).

Tuberculosis in elephants

Tuberculosis can be a debilitating disease for all species, but it is not necessarily fatal. It has a variety of effects on the body, and has different effects on different individuals. Symptoms common to both humans and elephants may include weight loss, anorexia, weakness, coughing, and difficulty breathing (Gutter, 1981; Binkley, 1997; Mikota et al., 2001). Diagnosis of tuberculosis in elephants is most often made post-mortem. Clinical signs of tuberculosis generally do not occur ante-mortem unless the infection is advanced (Francis, 1958). Elephants brought to veterinarians for treatment of symptoms including weight loss, increased water intake, increased urination, atrophied muscles, depression, and loss of appetite (Gutter, 1981; Saunders, 1983; Binkley, 1997) were found to be infected with *M. tuberculosis* only after their deaths.

M. tuberculosis is common in captive elephants. In North America, 18 of 359 (3.3%) captive elephants surveyed between August 1996 and May 2000 were afflicted with tuberculosis (Mikota et al., 2000). *M. tuberculosis* was found in 24 captive elephants in California, Illinois, Arkansas, Missouri, Florida, and New Mexico between 1994 and 2001 (Payeur et al., 2002). A study of elephants in North American zoos recorded 8 of 379, or 2.1%, deaths caused by tuberculosis, ranging from prior to 1941 to 2001 (Mikota et al., 2001). Most captive elephants with tuberculosis have been Asian

elephants. Since 2001, there has been only one reported case of tuberculosis in an African elephants (Urbain, 1938). In all cases of tuberculosis afflicting elephants, *M. tuberculosis* has been the responsible agent.

The source of tuberculosis for elephants and humans is uncertain. There are no reported cases of tuberculosis in wild elephants (Mikota et al., 2000). It is often difficult to diagnose tuberculosis in elephants while they are alive; without the corpse of an infected wild elephant, it may not be possible to determine incidence of infection.

Tuberculosis, as caused by *M. tuberculosis*, seems to be common in domestic animals and wild animals that have close contact with domestic animals. For example, when poultry and game birds contract tuberculosis, the causative agent is typically *M. avium-intracellularae* (Montali et al., 1976); when pet birds contract tuberculosis, the causative agent is typically *M. genavense* or *M. avium* (Hoop et al., 1996). There are, however, reports of pet birds, including a canary (*Serinus canaria*) and a Blue-fronted Amazon Parrot (*Amazona amazona aestiva*), becoming infected with *M. tuberculosis* as transmitted from their owners through coughing (Hoop, 2002). Humans also have been known to spread the disease to elephants.

There are no recorded instances in which an extant elephant has contracted *M. tuberculosis* without being in contact with a human (Mikota et al., 2000), but it is uncertain whether contact with infected humans is responsible for all the reports of *M. tuberculosis* in elephants.

Tuberculosis on bone

Rothschild and Martin (1993) reported that evidence of tuberculosis rarely shows

up on bone. Tuberculosis can react differently on different bones and on different areas of the same bone. Skeletal evidence for tuberculosis on humans is most often seen on ribs, vertebrae, and metacarpals; signature marks include granular masses, abscesses, necrosis, and subchondral articular surface undermining.

The exact mechanism by which *M. tuberculosis* causes bone breakdown is not fully understood. Nair et al. (1996) propose three possibilities: (1) bacteria liberate acid and proteases, directly destroying the non-cellular bone components; (2) bacteria initiate cellular processes that stimulate bone degradation; (3) bacteria inhibit the process of bone matrix synthesis, by either increasing osteoclast production or decreasing osteoblast production. In the human spine, *M. tuberculosis* infection decreases the extra-cellular matrix and collapses the vertebrae (Meghji et al., 1997). It is not known whether the bacterial infection causes bone breakdown directly, or if it is an indirect reaction to the introduction of a foreign agent into the cells.

Rothschild and Helbling (2001) examined 49 mastodons with foot bones available; 45% showed undermining. This feature was identical to patterns that they had interpreted as pathognomonic for tuberculosis in extinct bison. The undermining was unusual in that it did not preferentially affect mastodons based on age at death, body size, season of death, or location. The authors did not mention whether the data reflect gender differences. Twenty-five percent of examined specimens with both ribs and feet present had articular surface undermining on foot bones in addition to periosteal reaction of the ribs; periosteal rib reaction is a character commonly associated with tuberculosis (Rothschild and Martin, 1993).

Elephant foot care

One of the most important aspects in managing captive elephants is protecting their feet from harm. Caretakers spend more time on foot problems than on any other aspect of elephant care except feeding and cleaning. As the largest land animal on earth, the foot of the elephant has a substantial amount of weight to brace. Each foot of a 13,200 pound bull African elephant has to support 3300 pounds when stationary; when walking, each foot supports 4400 pounds; when ambling, each foot supports 6600 pounds. Because of the extreme amount of pressure placed on the elephant foot, any damage caused to the foot has serious repercussions for the mobility of the animal (Fowler, 2001).

There are several reasons for the frequent occurrence of foot problems in captive elephants, including: lack of exercise, overgrowth of nail and/or sole, improper enclosure surface, too much moisture, insufficient foot grooming, unsanitary enclosures, inherited poor foot structure, malnutrition, and skeletal disorders such as arthritis (Fowler, 2001). Wild elephants maintain their healthy feet by covering large distances daily to eat, bathe, dig, and dust; this exercise strengthens foot muscles and promotes good blood flow to the feet, which most captive elephants lack due to an inactive lifestyle (Roocroft and Oosterhuis, 2001).

MATERIALS AND METHODS

The material for this study was provided by the Michigan State University Museum Vertebrate Paleontology collection (MSUVP) and Mammal Research collection (MSUMR), the University of Michigan Museum of Zoology (UMMZ), the Field Museum of Natural History (FMNH), and the National Museum of Natural History (USNM) (Table 1). Fossil material includes American mastodon (*Mammut americanum*) post-cranial material, which was recovered in Michigan from various Late Pleistocene sediments. Recent material includes 10 Asian elephants (*Elephas maximus*) and 9

Table1. List of Specimens

Specimen #	Species	Sex	Habitat	Age	Undermining
FMNH 53749	*L. africana*	?	captive	adult	present
FMNH 60601	*E. maximus*	male	captive	adult	present
FMNH 49894	*E. maximus*	male	wild	adult	present
USNM 304615	*L. africana*	male	wild	adult	present
USNM 49489B	*L. africana*	?	?	adult	present
USNM 163318	*L. africana*	male	wild	adult	present
USNM 270993	*L. africana*	female	captive	adult	present
USNM 588113	*L. africana*	female	captive	adult	present
USNM 269391	*E. maximus*	?	wild	juvenile	absent
USNM 49639	*E. maximus*	?	captive	adult	present
USNM 49489	*L. africana*	?	captive	adult	present
USNM 20756*	*L. africana*	male	captive	juvenile	CO
USNM 240476*	*E. maximus*	female	wild	juvenile	CO
USNM 266911	*E. maximus*	female	captive	adult	present
MSUMR no #	*E. maximus*	?	captive	juvenile	absent
MSUMR 7550	*L. africana*	male	wild	adult	present
MSUVP 1289	*M. americanum*	?	wild	adult	present
UMMZ no #	*E. maximus*	female	captive	adult	present
UMMZ no data	*E. maximus* (?)	?	?	adult	present
UMMZ 157850	*E. maximus*	female	captive	adult	present

*CO = cannot obtain data from this specimen

African elephants (*Loxodonta africana*) with associated post-cranial material. Recent elephants specimens include those that died in captivity as well as in the wild.

The first part of the project included describing the character defined as pathognomonic for tuberculosis by Rothschild and Helbling (2001): articular surface undermining of foot bones, seen most frequently on metapodials. Mastodon metapodials were examined macroscopically for dimensions, position in the skeleton, description of articular surface undermining, and any other unique features present.

Once metapodial features were described in the mastodon, they were then compared to the metapodials of extant elephants, both African and Asian. Each metacarpal and metatarsal was macroscopically examined. Dimensions of the bones were recorded (Figure 11B) (Appendix A). Scaled photographs of each specimen were taken using a 35 mm Minolta Maxxum 5, and some measurements were made from the photographs in cases when it was not convenient to measure on site. The skeletal elements were identified and recorded as positive or negative for articular surface undermining and lipping of the articular surface. The articular surface was examined for the presence of pathologies. This was done to eliminate the possibility that the undermining was caused by spondyloarthropathy, which causes a bone reaction similar to articular surface undermining, but also affects the articular surface (Rothschild and Martin, 1993). Any other unusual characteristics were also noted.

Histograms were generated showing the percentage of each metapodial affected by undermining to determine if a particular metapodial preferentially shows the feature. The data were also sorted by sex, species, age at death, and whether the elephants were captive or wild, to determine whether the undermining is biased towards any or all of these criteria.

RESULTS

Metapodial features

Based on the examination of Recent elephant foot bones, there appears to be two distinguishing features on metapodials: (1) the undermining of the bone, which is expressed as a depression, or excavation, on the posterior side behind the articular surface (Figure 11C), and (2) the "lipping" of the articular surface, an overgrowth of the articular surface on the posterior side of the bone, that interrupts the smooth contact between the articular surface and the body of the foot bone (Figure 11D). These two characters do not necessarily appear concurrently; lipping of the articular surface may occur without the presence of excavation, though lipping always appears with excavation, as excavation appears to be an extension of this character.

Articular surface undermining on mastodons

Rothschild and Helbling (2001) identified subchondral articular surface undermining on the metapodials of 22 mastodons, including MSUVP 1289 (Appendix A). This character was noted at the distal articular surface on the posterior facets. MSUVP 1289 is an American mastodon of Late Pleistocene age from Ottawa County, Michigan; it was excavated by the Grand Rapids Public Museum from muck on top of light colored till in June of 1947 (Abraczinskas, 1993). Material found includes tusks, humerus, vertebrae, foot bones, ribs, pelvis, and leg bones. For this study, the foot bones of this specimen were chosen as a standard with which to compare extant elephant bones. Six foot bones were examined from MSUVP 1289, including metacarpals, metatarsals, and phalanges. The four metapodials show articular surface undermining, and no

pathologies are apparent on the articular surfaces. Neither phalanx has articular surface undermining, and no pathologies are apparent on the articular surfaces of either bone.

Description of elephant specimens

The Field Museum of Natural History has three specimens with associated foot bones (Appendix A). FMNH 53749 is an African elephant of unknown sex from the Chicago Zoological Society. It was obtained by the Field Museum in July of 1943. Material studied includes 1 phalanx, 4 metapodials, and one tarsal. Articular surface undermining and lipping of the articular surface is present on RP-PPIV and R-MCIII. Lipping of the articular surface is present on R-MCII, L-MTII, and L-MTIV. There is neither undermining nor lipping on L-CAL. None of the listed bones have articular surfaces apparently affected by pathologies.

FMNH 60601 is a male Asian elephant from the Chicago Zoological Society named "Ziggy." Ziggy was obtained by the Field Museum in October 1975. Material studied includes 1 phalanx and 12 metapodials. Articular surface undermining and lipping of the articular surface is present on R-MCII, R-MCIII, R-MCIV, R-MCV, L-MCII, L-MCIV, L-MCV, R-MTII, R-MTIII, L-MTII, L-MTIII, and L-MCV. Lipping of the articular surface is present on R-MTV and L-MTV. There is no undermining or lipping on LP-PPI. None of the listed bones have articular surfaces apparently affected by pathologies.

FMNH 49894 is a male mainland Asian elephant (*Elephas maximus indicus*) from Hardwar, Uttah Pradesh, India, collected by I.I. Hauser and obtained by the Field Museum on April 7, 1865. Material studied includes 11 metapodials. Articular surface

undermining and lipping of the articular surface is present on R-MCII, R-MCIII, R-MCIV, L-MCII, L-MCIII, R-MTII, R-MTIV, L-MTII, and L-MTIV. There is no undermining or lipping on R-MCV and L-MCV. None of the listed bones have articular surfaces apparently affected by pathologies. There is an ovular depression on the posterior side of R-MCIII, near the distal articular surface (Figure 10B).

The National Museum of Natural History collections includes 11 individuals with associated foot bones (Appendix A). USNM 304615 is a male African Elephant from Angola, district of Bie Cuando, in the region of Mancuso. It was collected at 17°19' S, 21°14' E, 48 miles north-northwest of Mancuso. Nine metapodials were available for study. R-MCIII, L-MCII, L-MCIV, R-MTII, L-MTI, L-MTII and L-MTIII show both lipping and excavation. L-MCV shows lipping; R-MCI has no articular surface undermining. None of the listed bones have articular surfaces apparently affected by pathologies.

USNM 49489B has no data, but is likely an African elephant, based on its large size and comparatively slender foot bones. Foot bones available for study include 19 metapodials. The articular surfaces for R-MCIII, R-MCIV, L-MCIII, L-MCIV, and L-MTII have been detached from the rest of the bone, so articular surface undermining data is not obtainable from these bones. R-MCI, L-MCI, R-MTIII, R-MTIV, L-MTIII, and L-MTIV show articular surface undermining. There is no undermining on R-MTI. The rest of the listed bones show minor lipping, but no excavation beneath the articular surface. None of the listed bones have articular surfaces apparently affected by pathologies.

USNM 163318 is a male African Elephant from Kenya. It was collected on the western slope of Mt. Kenia, at an altitude of 7000 feet. The elephant was added to the

collection on August 19, 1909, as part of the Smithsonian African Expedition, and was collected by Theodore Roosevelt. Foot bones available for this specimen include 14 metapodials. R-MCIII, R-MCIV, L-MCIII, L-MCIV, R-MTIII, R-MTIV, L-MTII, and L-MTIII show articular surface undermining and lipping of the articular surface. R-MCV, L-MCV, R-MTII, R-MTV, L-MTIV, and L-MTV show lipping of the articular surface. None of the listed bones have articular surfaces apparently affected by pathologies.

USNM 270993 is a female African elephant from the Philadelphia Zoological Gardens. She died on March 12, 1943. Foot bones available for this specimen include 14 metapodials and 1 phalanx. R-MCI, R-MCII, R-MCIII, R-MCIV, L-MCI, L-MCII, L-MCIII, L-MCIV, R-MTIII, L-MTIII, and L-MTIV articular surface undermining, and lipping of the articular surface. R-MCV, L-MCV, R-MTIV, L-MTIV, and LM-PPV show lipping of the articular surface. None of the listed bones have articular surfaces apparently affected by pathologies.

USNM 588113 is a female African elephant from an unknown locality who died in captivity at the National Zoological Park. Her remains were added to the collections on August 22, 2000, from an unknown collector. In life, this elephant had foot problems, and post-death examination revealed that she had tuberculosis, though it was not ruled as the cause of death (Linda Gordon, personal communication). Foot bones examined from this specimen are 4 metapodials and 5 phalanges. R-MTI, R-MTII, R-MTIV, RP-PPII, and RP-PPIII show articular surface undermining and lipping of the articular surface (Figure 11E). There is no articular surface undermining or lipping of the articular surface on R-MTV, RP-PPIV, and LM-IPIV. All listed bones have articular surfaces apparently unaffected by pathologies, and are significantly more porous than bones of other

elephants examined (Figure 12A). R-MTII shows a separation between the articular facets on the distal portion of the bone (Figure 12B). The degree of undermining present, however, is not vastly different than the other specimens.

USNM 269391 is a juvenile Asian elephant collected by G.S. Huntington. No locality information is provided for this specimen, which was obtained from the Army Medical Museum, U.S. War Department. Foot bones examined for this specimen include 18 metapodials. Articular surfaces for all listed bones are deformed in some way, as sesamoid bones that were glued to the surface either fell off or were removed, leaving residue behind or taking part of the articular surface away. The following bones from this specimen are missing their distal articular surfaces: R-MCIII, R-MCIV, R-MCV, L-MCII, L-MCIII, L-MCIV, L-MCV, R-MTIII, R-MTIV, L-MTI, L-MTIII, L-MTIV, and L-MTV. Of the bones whose distal articular surfaces were still attached to the body of the bone, there is no articular surface undermining on R-MCII, R-MTII, and L-MTII. There is minor lipping of the articular surface on R-MTI and L-MTII.

USNM 49639 is an Asian elephant of unknown sex. The specimen locality is unknown, as is the collector. The individual died on Nov. 6, 1898, at the National Zoological Park. Bones available for this specimen include 20 metapodials. All of the bones have a distinct "bunching" that surrounds the bone directly proximal to the articular surface (Figure 12C); the bunching is porous in nature. This feature makes articular surface undermining difficult to identify. Articular surface undermining and lipping of the articular surface is present on L-MCIV, R-MTI, R-MTIII, R-MTV, L-MTI, and L-MTIII. There is no articular surface undermining on R-MCI, R-MCIV, L-MCI, L-MCII, L-MCV, R-MTIV, and L-MTV. There is lipping of the articular surface on R-

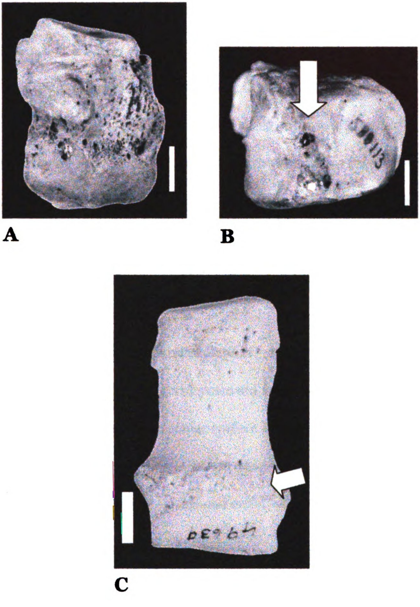


Figure 12. (A) USNM 588113 R-MTV (posterior view). Note the increased amount of pores on this bone. (B) USNM 588113 R-MTIV (distal view). Arrow denotes the location of the separation of articular facets. (C) USNM 49639 L-MTII (anterior view). Arrow denotes the location of "bunching." Scale bar = 2 cm.

MCII, R-MCIII, R-MCV, L-MCIII, R-MTII, L-MTII, L-MTIV. The articular surfaces of all listed bones are apparently unaffected by pathologies.

USNM 49849 is an African elephant of unknown sex collected by Dr. S Schuenland in South Africa, Cape Colony, Addo Bush, near Port Elizabeth. Only the right forelimb and right hind limb are present; the remaining two limbs are on loan. The legs are fully articulated. R-MTI is absent from the articulated foot, and R-MTII is missing its articular surface. Articular surface undermining is present on R-MTIII, R-MTIV, and R-MTV. There is no articular surface undermining on R-MCI. Slight lipping of the articular surface is present on all other bones. None of the bones show excavation beneath the articular surface. None of the articular surfaces appear to be affected by pathologies.

USNM 20756 is a male African elephant named "Mungo." He died in captivity on April 6, 1882, when he was about 5 years old, and was presented to the museum by Adam Fovepaugh. Evidence of articular surface undermining is unobtainable from this specimen, as the distal articular surfaces are detached from the body of the foot bone. There is porous bone near the proximal and distal surfaces of the metapodials; the nature of the bone here is similar to that shown in USNM 588113, but to a lesser degree.

USNM 240476 is a juvenile Asian elephant collected in Annam, Vietnam, 20 miles northeast of Vinh, by F.R. Wilsin in 1924, as part of the National Geographic expedition to central Asia. As in USNM 20756, no foot bones have distal articular surfaces fused to the body of the bone. Again, there is porous bone present near the proximal and distal articular surfaces of the metapodials.

USNM 266911 is a female Asian elephant who died on August 12, 1937, in the

National Zoological Park. Foot bones examined for this specimen include 9 metapodials. All metapodials show bunching near the distal articular surfaces on both the posterior and anterior sides. The metacarpals show a more extreme degree of bunching than do the metatarsals. All metapodials present (R-MCI, R-MCII, R-MCIII, R-MCIV, R-MCV, R-MTII, R-MTIII, R-MTV, and L-MTIV) show articular surface undermining and lipping of the articular surface. No pathologies are apparent on the articular surfaces. R-MCIII has a depression on the posterior side, near the distal articular surface.

The mammal collections at Michigan State University hold two recent elephant skeletons with associated foot bones (Appendix A). The first does not have a catalogue number. It is a juvenile Asian elephant, possibly from a circus. The specimen consists of four articulated legs, which included R-MCI, R-MCII, R-MCIII, R-MIV, R-MCV, L-MCI, L-MCII, L-MCIII, L-MCIV, L-MCV, R-MTI, R-MTII, R-MTIII, R-MTIV, L-MTI, L-MII, L-MTIII, and L-MTIV. Most of the articular surfaces are detached from the foot bone with which they are associated. For the bones that have their articular surfaces intact, R-MCI, R-MCV, L-MCI and L-MCV show no articular surface undermining. None of the listed foot bones have articular surfaces apparently affected by pathologies.

MSUMR 7550 is a wild male African elephant that was at least 20 years old at death. He was collected in Kenya, 35 miles north of Voi by Jens Touborg on February 2, 1962. The specimen is mounted on exhibit at the Michigan State University Museum; nearly all skeletal elements are present. In the feet, the only apparent bone missing is R-MCI. Of the available bones, R-MCII, R-MCII, R-MCIV, L-MCII, L-MCIII, L-MCIV, R-MTII, R-MTIII, R-MTIV, R-MTV, L-MTI, L-MTIII, L-MTIV, and L-MTV have articular surface undermining and lipping of the articular surface. R-MCV, L-MCI, L-MCV, and

L-MTII show lipping only. R-MTI has neither feature. None of the listed bones have articular surfaces apparently affected by pathologies. In this specimen, the metatarsals have a greater degree of undermining than do the metacarpals. On the metacarpals, both the R- and L-MCIV have a greater degree of undermining than the other metacarpals.

The University of Michigan Museum of Zoology has three elephants with associated foot bones (Appendix A). Two do not have catalogue numbers. The first of these (referred to as UMMZ no number) is "Amber," an adult female Asian elephant from the Toledo Zoo. Metapodials available for study are R-MCI, L-MCI, R-MCII, L-MCII, L-MCIII, and L-MCIV. All listed bones have articular surface undermining except for R-MCI, which has lipping of the articular surface only. None of the listed bones have articular surfaces apparently affected by pathologies. The proximal articular facets on R-MCII and L-MCII overlap each other, giving the bone a "squished" appearance. R-MCI has separated distal articular facets.

The second UMMZ specimen with no number (referred to as UMMZ no data), has no associated data. It is an adult, and likely an Asian elephant. Metapodials available for examination are L-MTI, L-MTII, L-MTIII, L-MTIV, and L-MTV. All listed bones have articular surface undermining. L-MTII and L-MTIV have small holes on the distal articular surfaces. The rest of the listed bones have articular surfaces apparently unaffected by pathologies. The metapodials on this individual, along with UMMZ 157850, have the most drastic articular surface undermining of any in this study; L-MTIII and L-MTIV have the most extreme undermining. The bones are extremely porous, and resemble those of USNM 588113. On this specimen, the tarsus also exhibits extreme articular surface undermining.

UMMZ 157850 is "Minnie," an adult female Asian elephant from the Brookfield Zoo. Bones available for examination include most of the right hind foot and the left forefoot. Butchering post-death removed parts of the foot; R-MCIV is mostly gone, and R-MCIII and L-MCV are missing most of their distal articular surfaces. All examined bones show articular surface undermining except for R-MTV and R-MTI. The metapodials on this individual have drastic undermining, most notably R-MTIV. The articular surface of L-MCII is slightly chipped. Many of the bones are porous, especially R-MTI. The remaining bones have articular surfaces apparently unaffected by pathologies.

Frequency of undermining on foot bones

Of the 19 extant elephants examined (Table 1), 17 had foot bones with at least some associated distal articular surfaces intact. From these 17 elephants, 173 bones were examined. Of these, 7 are phalanges, one is a tarsal, 86 are metacarpals, and 79 are metatarsals. Forty-three percent (3 of 7) of phalanges have articular surface undermining; the tarsal did not have articular surface undermining. Of the 165 metapodials, 141 (85%) have articular lipping of the articular surface (Figure 13A) (Table 2); 103 (62%) are affected by articular surface undermining and lipping of the articular surface (Figure 13B) (Table 2). Eighty-three percent (71 of 86) of metacarpals have lipping of the articular surface (Figure 14A) (Table 2); 59% (51 of 86) of metacarpals have articular surface undermining and lipping of the articular surface (Figure 14B) (Table 2). Eighty-nine percent (70 of 79) of metatarsals have lipping of the articular surface (Figure 15A) (Table 2). Sixty-six percent (52 of 79) of metatarsals have

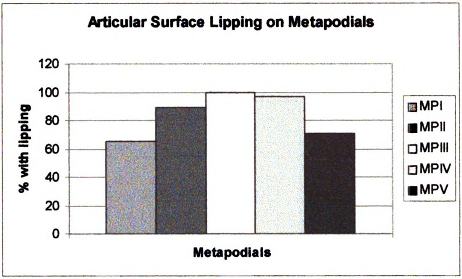
articular surface undermining and lipping of the articular surface (Figure 15B) (Table 2).

A chi-square test applied to the metacarpals affected with articular surface undermining reveals that, at the 0.05 level, the distribution of articular surface undermining on metacarpals is significantly different from a random distribution. Application of the same test to the metatarsals also reveals that, at the 0.05 level, the distribution of articular surface undermining on metatarsals is significantly different from a random distribution (Appendix B).

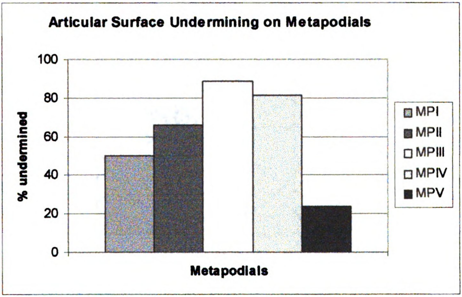
Articular surface undermining shows up most frequently on the third metapodial (31 of 35; 89%) (Table 2) (Figure 13). A chi-square test applied to the metapodial data revealed that at the 0.05 level, the distribution is significantly different from random (Appendix B). Every elephant that has articular surface undermining has both L- and R-MCIII and L- and R-MTIII affected except for two, USNM 49489 and USNM 49639. These two elephants show some lipping on the manus, but no undermining. The hind feet of USNM 49489 show undermining. The R-MTIII is affected; the L-MTIII was not available for study on this specimen. The hind feet of USNM 49639 also show undermining, on both L-MTIII and R-MTIII. The metatarsals were frequently affected to a greater degree than the metacarpals.

Articular surface undermining preferentially affects MTIII on the pes (Figure 15), but on the manus MCII, MCIII, and MCIV are nearly equally affected (Figure 14). A chi-square test applied to the MCII, MCIII, and MCIV data reveals that the distribution of undermining on these bones is not significantly different from a random distribution. A chi-square test applied to MTII, MTIII, and MTIV reveals that at the 0.05 level, the data are significantly different from random (Appendix B).

Table 2. Summary of examined foot bones.					
Affected Bone	# Present	# with Lipping	% with Lipping	# with ASU	% with ASU
Hindlimb					
CAL	1	0	0	0	0
MTI	10	7	70	6	60
MTII	19	17	89.47	11	57.89
MTIII	18	18	100	17	94.44
MTIV	17	17	100	13	76.47
MTV	15	11	73.33	5	33.33
PPI	1	0	0	0	0
PPII	1	1	100	1	100
PPIII	1	1	100	1	100
PPIV	2	1	50	1	50
PPV	0	0	0	0	0
Forelimb					
MCI	16	10	62.5	7	43.75
MCII	19	17	89.47	14	73.68
MCIII	17	17	100	14	82.35
MCIV	15	14	93.33	13	86.67
MCV	19	13	68.42	3	15.79
PPI	0	0	0	0	0
PPII	0	0	0	0	0
PPIII	0	0	0	0	0
PPIV	0	0	0	0	0
PPV	1	1	100	0	0
IPIV	1	0	0	0	0
Total	173	145	83.82	106	61.27
Metapodials only	165	141	85.45	103	62.42

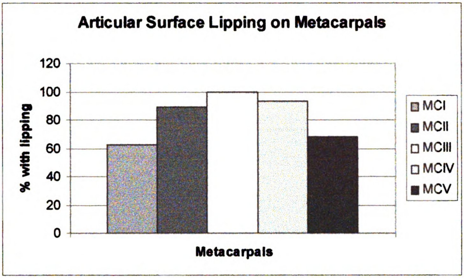


A. Percentage of metapodials affected by articular surface lipping.

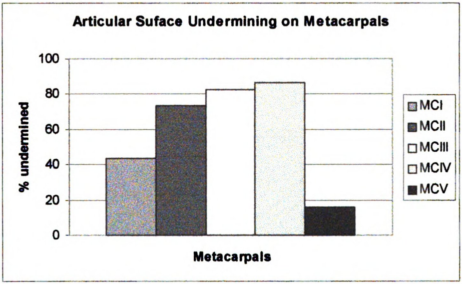


B. Percentage of metapodials affected by articular surface undermining and lipping of the articular surface.

Figure 13. Summary of metapodials affected by (A) lipping of the articular surface and (B) articular surface undermining.

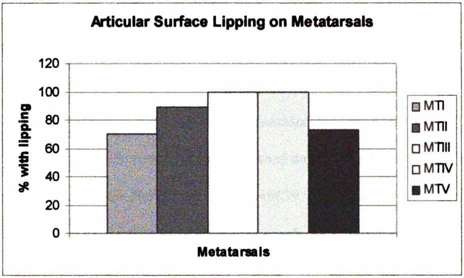


A. Percentage of metacarpals affected by articular surface lipping.

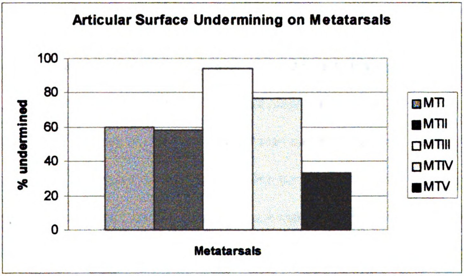


B. Percentage of metacarpals affected by lipping of the articular surface and articular surface undermining.

Figure 14. Summary of metacarpals affected by (A) lipping of the articular surface and (B) articular surface undermining.



A. Percentage of metatarsals affected by lipping of the articular surface.



B. Percentage of metatarsals affected by lipping of the articular surface and articular surface undermining.

Figure 15. Summary of metatarsals affected by (A) lipping of the articular surface and (B) articular surface undermining.

Preferential occurrences of undermining

Adult wild elephants (n=4) and adult captive elephants (n=9) show similar degrees of undermining (Table 1). Captive elephants have additional malformations, most notably the "bunching" of the bone around the distal articular surface, on both the anterior and posterior side of the bone, and the increased porosity of the bones. The bunching has an appearance similar to a sock pushed down around the ankle. This character appears in USNM 266911 and USNM 49639. The bunching distorts the bone in the same area that would show articular surface undermining and lipping, if they were present.

In the wild, both adult African (n=3) and adult Asian (n=1) elephants have similar degrees of articular surface undermining. Captive adult African (n=2) and adult Asian (n=4) elephants also have similar degrees of undermining (Table 1).

Male and female elephants are equally affected by articular surface undermining (Table 1). One hundred percent of the adult male elephants (n=5) exhibit articular surface undermining: three of these are wild African elephants, one is a wild Asian elephant, and one is a captive Asian elephant. One hundred percent of the adult females (n=5) show articular surface undermining: two are captive adult African elephants, and three are captive adult Asian elephants.

Of the elephants in this study, four are juveniles. Of these four, one is a captive male African elephant of about 5 years in age; one is a wild female Asian elephant; one is a captive elephant of unknown sex; and one is a wild Asian elephant of unknown sex. The un-fused epiphyses on the metapodials from the female African and female Asian elephant were not found associated with the associated bone body, or were reattached to

the body of the bone post-mortem in a destructive manner. On those two, lipping cannot be identified, and there is no evidence of undermining. Neither of the two with articular surfaces intact show undermining; at best, there is the slightest evidence of articular surface lipping. All of the adults (n=15) included in this study show articular surface undermining or lipping of the articular surface (Table 1).

DISCUSSION

Frequency of undermining

The lipping of the articular surface is present on 85% (141 of 165) of all metapodials examined in this study. Sixty-two percent (103 of 165) of these metapodials show, in addition, the character of articular surface undermining; twenty-three percent (38 of 164) show lipping of the articular surface only. The remaining bones (24 of 165; 15%) show neither undermining nor lipping. Rothschild and Helbling (2001) reported that articular surface undermining indiscriminately affected mastodons in their study regardless of age at death, body size, season of death, or location. For Recent elephants, this does not appear to be true. Articular surface undermining is present on at least one metapodial from every adult elephant in this study. The juvenile elephants show no articular surface undermining; if there is any restructuring on the foot bones, it is a slight lipping of the articular surface without undermining involved. The occurrence of articular surface undermining of Recent elephants is biased towards adults, suggesting a strong relation to ontogeny.

Articular surface undermining preferentially affects the third metapodial, which is the longest and most centrally positioned (Figure 12). Assuming a weight of 15,000 pounds for the largest African elephant, with a slipper area (sole) of 254 square inches (Fowler, 2001), the pressure on the elephant foot can reach nearly 15 pounds per square inch. Most of this weight is centered on the third metapodial, due to the elephant's mesaxonic limb structure. Marsh (1884) devised a classification system for ungulates based on functional limb symmetry. This classification, as described by Klaits (1972), can be applied to proboscideans, which are mesaxonic because the axis of the limb

can be applied to proboscideans, which are mesaxonic because the axis of the limb passes through the longest, centralized digit: the third. As the foot contacts the ground, torsion of the leg is produced, causing the first row of carpals or tarsals to apply pressure to the second row (Cope, 1887). The combination of immense weight, columnar legs, and overall limb structure of the proboscideans that show the highest degree of undermining on their third metapodials suggests that the undermining is actually restructuring of bone related to pressure. Furthermore, articular surface undermining does not occur on juvenile individuals, although some juveniles do show lipping of the articular surface. Lipping is suggested to be the first stage in restructuring the foot bone, eventually culminating in undermining. Even a young elephant carries a large amount of weight on its skeleton, but seemingly not enough to cause undermining. As the elephant grows larger, more pressure is applied to the feet, and the bones continue to restructure.

Articular surface undermining occurs with a higher frequency on MTIII than on MCIII (Figures 14 and 15). The semi-digitigrade stance of the forelimbs may cause more stress to the foot bones than the semi-plantigrade stance of the hind limbs, causing the metatarsals to be restructured more often than metacarpals.

The hind feet almost always have a greater role in propulsion than do the fore feet, though in the symmetrical elephant gait, the intervals between contact of the fore and hind limbs is about equal (Hildebrand, 1976). When an elephant ambles, the forward swing of the hind leg has slightly more kinetic energy than the foreleg. The difference is kinetic energy is due to the small difference in mass between the hind and fore leg; the foreleg of the elephant, at approximately 250 kg, is slightly lighter than the hind leg, at 268 kg (Hildebrand and Hurley, 1985). Increased mass on the hind leg results in greater of undermining on MTIV and MTV, as compared with MCIV and MCV, suggests that the presence and degree of undermining is an effect of how the weight of an elephant is supported by its skeletal anatomy.

Articular surface undermining preferentially affects MTIII on the pes (Figure 15), but on the manus MCIII and MCIV are nearly equally affected (Figure 14). The burden of support on the mesaxonic manus, then, may not be primarily MCIII. Because MCIII and MCIV are affected by articular surface undermining to approximately the same degree, it appears that the combination of MCIII and MCIV provides the primary means of support. The rhinoceros manus, also mesaxonic, divides the burden of support between the second and third digits when the manus lifts, and the third and fourth digit when the digit manus lands (Klaits, 1972). The elephant manus, then, may still have a plane of structural symmetry through the middle digit, but this digit apparently acts in concert with the fourth digit.

The second metapodials in the manus and pes are also often affected by undermining, though not as frequently as the third and fourth metapodials (Figures 14 and 15). MCII is more frequently affected with undermining than MTII. These results suggest that pressure on the manus is more evenly distributed by the three centralized digits (MCII, MCIII, and MCIV). In the pes, however, the pressure from the limb is transmitted most heavily to the MTIII (Figure 15), as there is a wider gap between the percentage of affected MTIII and the percentages of affected surrounding metatarsals than there is between the percentage of affected MCIII and the percentages of affected surrounding metacarpals (Figure 14 and 15).

Articular surface undermining and taxon-specificity

Articular surface undermining is not species-specific. In captivity, Asian elephants appear to suffer more foot problems than African elephants (Fowler, 2001). It might be suggested, then, that Asian elephants would have a higher degree of articular surface undermining, but this is not true. In fact, all of the adult African (n=8) and Asian (n= 6) elephants in this study, both captive and wild, show articular surface undermining (Table 1).

These data support a structural origin for undermining. Both Asian and African elephants, related at the family level, are graviportal animals with mesaxonic limbs. The metapodials of African and Asian elephants are very similar in shape; their articulated feet, too, are nearly identical. The primary difference between the limbs of these two proboscidean genera is size; African elephants are generally larger.

Articular surface undermining and sexual dimorphism

Sexual dimorphism is present in elephants; the males are larger than the females within the same species. More pressure would be applied to the feet on a larger elephant than on the feet of a smaller elephant, so the larger, heavier males might be expected to show a higher frequency of articular surface undermining. However, for elephants whose sexes are known, the frequency of undermining between the sexes is the same. One hundred percent of adult males (n=5, Table 1) and adult females (n=5, Table 1) exhibit articular surface undermining.

Articular surface undermining and age

Four elephants in this study are juveniles. Of these four, one is a captive male African elephant of about 5 years in age (USNM 20756), one is a wild female Asian elephant (USNM 240476), one is a captive elephant of unknown sex (MSUMR no #), and one is a wild Asian elephant of unknown sex (USNM 269391). The female African and female Asian elephant do not have intact articular surfaces (Table 1). On these two specimens, lipping cannot be identified, and there is no evidence of undermining. Neither of the two juveniles with articular surfaces intact show undermining; at best, there is the slightest evidence of articular surface lipping. In contrast, 100% of adult elephants included in the study (n=15) have at least one metapodial with articular surface undermining or lipping of the articular surface. The juveniles in this study were too young to have fused epiphyses, which is why the articular surfaces were often absent or not strongly attached to the body of the bone. Until the individual becomes an adult, articular surface undermining might not have a chance to completely restructure the bone. Also, as a juvenile, the individual is apparently not large enough for the bone to begin to restructure. Articular surface undermining, then, is likely only found on larger, mature individuals.

Articular surface undermining and habitat

The potential relationship of articular surface undermining to habitat of the individual cannot be assessed using the data available in this study. Several of the elephant skeletons had no accompanying location data; of the 6 with location data, 2 are savanna African elephants from Kenya, 1 is a savanna African elephant from Angola, 1 is a savanna African elephant from South Africa, 1 is a mainland Asian elephant from Uttah Pradesh, and 1 is a mainland Asian elephant from Vietnam. All show articular surface undermining except for one juvenile mainland Asian elephant, from which articular surface undermining data could not be obtained. More data are needed to establish whether a relationship exists between articular surface undermining and habitat.

The presence of articular surface undermining is not related to whether the individual is enclosed in a captive habitat (Table 1). The adult captive elephants (n=9) in this study show severe metapodial undermining. After years in captivity, this is expected for an elephant (Fowler, 2001). Adult wild elephants (n=4), however, also show articular surface undermining. The nature and degree of undermining on the metapodials of the captive and wild elephants is comparable, suggesting that the occurrence of such a malformation is caused by the weight of the animal rather than by an outside factor; it is likely a feature of elephant skeletal anatomy, rather than a result of years in captivity. It is possible that captivity increases the likelihood that undermining would be present at an earlier age, or in smaller individuals, but the sample size is not large enough to support or refute this claim. To explore this idea further, the data must include wild adult females and more juveniles.

A character that is likely a result of years in captivity is the "bunching" appearance of the bone around the distal articular surface, on both the posterior and anterior side (Figure 12C), found in this study exclusively in captive individuals. The bunching distorts the bone in the same area that would show articular surface undermining and lipping, if present. Bunching, like undermining, could be a result of the pressure from the weight of the animal on the metapodials. It may be evidence of a stress

fracture, as a similar feature on a ceratopsian phalanx was described as such (Rothschild, 1988). This feature appears on the anterior side of metapodials from several wild individuals in this study, including the mastodon. The extreme development of this feature on captive individuals in this study, however, may relate to the increased sedentary lifestyle of the captive elephant, and is likely an abnormal part of proboscidean anatomy.

The argument for sexual dimorphism would be clarified by comparing elephants from equivalent situations. All adult females from which data were available in this study were captive. Captive elephants have more stress placed upon their feet due to lack of exercise. Captivity may compensate for smaller body size, causing undermining on the metapodials of females in this study. This idea should be revisited with data including wild female elephants, for comparison.

Articular surface undermining and tuberculosis in Recent proboscideans

Rothschild and Helbling (2001) suggested a causal connection between articular surface undermining and tuberculosis in fossil proboscideans. This relationship is not supported for Recent elephants. USNM 58813 is a female captive African elephant that suffered from tuberculosis. This specimen showed undermining; the undermining, however, was not different in appearance from the other adult elephants with articular surface undermining. Captive elephants are already at high risk for foot problems, due to lack of exercise combined with the hard substrate of most captive elephant habitats (Sadler, 2001). Tuberculosis may have weakened USNM 588113, and made it more difficult for her to get the proper exercise, but given the ubiquity of articular surface

undermining among non-tuberculin elephants, undermining was likely not a direct result of the tuberculosis.

Articular surface undermining and tuberculosis in fossil proboscideans

Rothschild et al. (2001) defined articular surface undermining as the pathognomonic character of tuberculosis in extinct bison skeletal material. Although bison and proboscideans are both graviportal animals, the bison foot does not function in the same way as the proboscidean foot. The elephant manus rotates upon a medial axis when the elephant takes a step. The bison has paraxonic limbs, like most members of the Order Artiodactyla (Klaits, 1972), and is not, then, primarily supported by a single metapodial (or three central metapodials) as is the proboscidean foot; rather, the axis of symmetry on the bison foot is between the two middle digits. In addition, the bison has unguligrade feet, as opposed to the semi-digitigrade and semi-plantigrade stances of the elephant fore- and hind feet, respectively. Because of these anatomical differences, the skeletal elements in the feet of the two animals likely react to stresses differently; therefore, inferred effects of tuberculosis on bison metapodials is not the best model for identifying the potential effects of tuberculosis on proboscidean metapodials.

CONCLUSIONS

This study of 165 metapodials belonging to 17 individual elephants revealed articular surface undermining and lipping of the articular surface in 62% (103 of 165) of the metapodials; 88% (15 of 17) of the elephants in this study had at least one metapodial with articular surface undermining and lipping of the articular surface. All affected elephants are adults, both males and females; no juveniles with intact articular surfaces (n=2) show undermining. Articular surface undermining is widespread in Recent adult elephants; it is not sex-specific, habitat-specific, or species-specific.

The third metapodial is most commonly affected by articular surface undermining (Figure 13); this increased frequency may be related to the fact that this metapodial receives the most pressure from the 10,000-plus pound animal with mesaxonic limbs. Articular surface undermining shows up more frequently on MTIII than on MCIII. Its presence on the MTIII of one specimen (USNM 49639) and absence on the MCIII of the same individual suggests that the pressure applied to the hind foot may be greater than that applied to the fore foot. This differential occurrence of articular surface undermining is likely related to the semi-plantigrade stance of the pes, compared to the semi-digitigrade stance of the manus. In a comparison of all elephants, the MTIII (pes) and MCIV (manus) most frequently show undermining. The three central metapodials provide the main support for the graviportal animal, especially in the elephant manus; MCIV and MCII are more often affected by undermining than MTIV and MTII, and MTIII is affected by undermining more often than MCIII (Appendix, Table B).

On the forefoot, MCIII shares the brunt of the pressure with MCIV, to a greater degree than MTIII shares the pressure with MTIV on the hind foot. The same distribution is observed in the mesaxonic limbs of the rhinoceros (Klaits, 1972), in which the plane of functional symmetry is through the third digit, but the third digit shares the burden of weight with the fourth and second digit, respectively, when the manus lands and when the manus raises. When the rhinoceros stands, the burden of support is shared by the third and fourth digit. For the Recent elephants in this study, MCII is also more often affected than MTII. This suggests that, on the manus, the pressure is more evenly distributed between the three central digits. On the pes, the difference between the percentage of bones with undermining between MTIII and the immediately surrounding digits is greater than the difference in percentage of bones with undermining between MCIII and the immediately surrounding digits, suggesting that the MTIII takes on a disproportionate amount of pressure.

In conclusion, articular surface undermining is widely developed in Recent adult elephants, and its presence is most reliably predicted by the age of the individual. The frequency of articular surface undermining is highest on foot bones that bear the greatest stress, suggesting a structural explanation for the observed frequency and distribution of the feature.

Future work

The results in this study suggest several avenues for future work: (1) Increase the sample size to further elaborate on the patterns that have been suggested in this thesis. (2) Pursue the possible link between habitat and the presence or degree of articular surface undermining. In Recent elephants, the slippers are softer for forest elephants, and rougher for desert elephants (Roocroft and Oosterhuis, 2001); it is possible that the

hardness of the substrate is related to the presence or degree of undermining in individuals. In captivity, most elephants reside in habitats with concrete or asphalt floors (Roocroft and Oosterhuis, 2001); these substrates exert additional pressure onto the foot of the individual (Sadler, 2001). Although there is no discernable difference in the appearance of undermining observed in captive and wild elephants examined for this study, it would be interesting to test this idea with elephants from a wider range of habitats. (3) Apply the methods in this study to metapodials of other extinct proboscideans. It would be most interesting to compare the results of this study with a similar study done on *Mammuthus*, considering the phylogenetic relationship between mammoths and elephants. (4) Conduct a microbiological test of the bone in the area where undermining is present (as performed by Rothschild et al. [2001], on bison metacarpals) to clarify where *M. tuberculosis* is present.

APPENDIX

Appendix A. Summary of examined foot bones

ASU = articular surface undermining				NU = no undermining present		
AAS = affected articular surface				U = undermining present		
CO = cannot obtain data from this specimen				L = lipping present (no undermining)		
Y = yes				IM = indeterminate measurement		
N = no						
Specimen #	Bone	ASU	AAS	Length (cm)	Width (cm)	L/W
FMNH 53749	L-CAL	NU	N	17.3	8	2.1625
FMNH 53749	R-MCIII	U	N	14.3	4.3	3.3255814
FMNH 53749	L-MCI	U	N	8	3.5	2.2857143
FMNH 53749	L-MTII	L	N	7.3	3	2.4333333
FMNH 53749	L-MTIII	L	N	9	3.5	2.5714286
FMNH 53749	RP-PPIV	L	N	8.5	3.5	2.4285714
FMNH 60601	R-MCIII	U	N	23.2	7.4	3.1351351
FMNH 60601	R-MCIV	U	N	22.5	8	2.8125
FMNH 60601	R-MCV	U	N	14.5	5.5	2.6363636
FMNH 60601	L-MCII	U	N	IM	7	IM
FMNH 60601	L-MCIV	U	N	22.5	8	2.8125
FMNH 60601	L-MCV	U	N	14.3	6	2.3833333
FMNH 60601	R-MTIII	U	N	16.3	6	2.7166667
FMNH 60601	R-MTV	L	N	11	7	1.5714286
FMNH 60601	L-MTII	U	N	IM	6	IM
FMNH 60601	L-MTIII	U	N	16.5	6	2.75
FMNH 60601	L-MTV	L	N	11	7	1.5714286
FMNH 60601	LP-PPI	NU	N	9	6	1.5
FMNH 49894	R-MCII	U	N	22	9	2.4444444
FMNH 49894	R-MCIII	U	N	23.5	8.5	2.7647059
FMNH 49894	R-MCIV	U	N	21.3	8.5	2.5058824
FMNH 49894	R-MCV	NU	N	15.3	9	1.7
FMNH 49894	L-MCII	U	N	21	7.75	2.7096774
FMNH 49894	L-MCIII	U	N	23.3	9	2.5888889
FMNH 49894	L-MCV	NU	N	16	8	2
FMNH 49894	R-MTII	U	N	14	6.3	2.2222222
FMNH 49894	R-MTIV	U	N	22	8.3	2.6506024
FMNH 49894	L-MTII	U	N	14.5	6	2.4166667
FMNH 49894	L-MTIV	U	N	14	6.3	2.2222222
USNM 304615	R-MCI	NU	N	12.8	5	2.56
USNM 304615	R-MCIII	U	N	25.4	7.4	3.4324324
USNM 304615	L-MCII	U	N	23.8	6.8	3.5
USNM 304615	L-MCIV	U	N	23.3	6.7	3.4776119
USNM 304615	L-MCV	L	N	21.1	6.5	3.2461538
USNM 304615	R-MTII	U	N	15.1	7	2.1571429
USNM 304615	L-MTI	U	N	8.5	3	2.8333333
USNM 304615	L-MTII	U	N	16.6	5.5	3.0181818
USNM 304615	L-MTIII	U	N	18.8	6.5	2.8923077
USNM 49489B	R-MCI	U	N	8.4	4	2.1

USNM 49489B	R-MCII	L	N	17	5.5	3.0909091
USNM 49489B	R-MCIII	CO	N	17.8	5.4	3.2962963
USNM 49489B	R-MCIV	CO	N	16.5	5.5	3
USNM 49489B	R-MCV	L	N	12.6	6	2.1
USNM 49489B	L-MCI	U	N	8.5	3.5	2.4285714
USNM 49489B	L-MCII	L	N	15.5	5	3.1
USNM 49489B	L-MCIII	CO	N	18.7	5.8	3.2241379
USNM 49489B	L-MCIV	CO	N	15.5	5.9	2.6271186
USNM 49489B	L-MCV	L	N	14.4	6.1	2.3606557
USNM 49489B	R-MTI	NU	N	5	2.5	2
USNM 49489B	R-MTII	L	N	9.5	3.7	2.5675676
USNM 49489B	R-MTIII	U	N	12.5	5	2.5
USNM 49489B	R-MTIV	U	N	10.6	4.6	2.3043478
USNM 49489B	R-MTV	L	N	7.6	5	1.52
USNM 49489B	L-MTII	CO	N	9.5	3.6	2.6388889
USNM 49489B	L-MTIII	U	N	13.2	4.5	2.9333333
USNM 49489B	L-MTIV	U	N	12	4.9	2.4489796
USNM 49489B	L-MTV	L	N	7.4	6.2	1.1935484
USNM 163318	R-MCIII	U	N	19	6.3	3.015873
USNM 163318	R-MCIV	U	N	17	5.5	3.0909091
USNM 163318	R-MCV	L	N	16.2	6.8	2.3823529
USNM 163318	L-MCIII	U	N	18.6	7	2.6571429
USNM 163318	L-MCIV	U	N	16.5	6.1	2.704918
USNM 163318	L-MCV	L	N	13.1	6	2.1833333
USNM 163318	R-MTII	L	N	11.5	3.5	3.2857143
USNM 163318	R-MTIII	U	N	13.5	6	2.25
USNM 163318	R-MTIV	U	N	13.4	5.4	2.4814815
USNM 163318	R-MTV	L	N	7.7	6	1.2833333
USNM 163318	L-MTII	U	N	11	4.4	2.5
USNM 163318	L-MTIII	U	N	13.5	5.1	2.6470588
USNM 163318	L-MTIV	L	N	12.2	4	3.05
USNM 163318	L-MTV	L	N	8.7	6.3	1.3809524
USNM 270993	R-MCI	U	N	7	3	2.3333333
USNM 270993	R-MCII	U	N	14.5	4.3	3.372093
USNM 270993	R-MCIII	U	N	15.2	4	3.8
USNM 270993	R-MCIV	U	N	14.5	4.4	3.2954545
USNM 270993	R-MCV	L	N	13	5	2.6
USNM 270993	L-MCI	U	N	6.8	3.4	2
USNM 270993	L-MCII	U	N	3.4	4.2	0.8095238
USNM 270993	L-MCIII	U	N	15.3	4.4	3.4772727
USNM 270993	L-MCIV	U	N	13.2	4.2	3.1428571
USNM 270993	L-MCV	L	N	12.5	3.5	3.5714286
USNM 270993	R-MTIII	U	N	10.5	3.3	3.1818182
USNM 270993	R-MTIV	L	N	9.2	3.5	2.6285714
USNM 270993	L-MTIII	U	N	10.5	3.2	3.28125
USNM 270993	L-MTIV	L	N	9.5	3.5	2.7142857
USNM 270993	LM-PPV	L	N	6	4	1.5
USNM 588113	R-MTI	U	N	6.5	3	2.1666667
USNM 588113	R-MTII	U	N	10	4	2.5
USNM 588113	R-MTIV	U	N	11.5	4.8	2.3958333

USNM 588113	R-MTV	NU	N	7.2	4.7	1.5319149
USNM 588113	RP-PPII	U	N	6.5	3.8	1.7105263
USNM 588113	RP-PPIII	U	N	6.7	3.8	1.7631579
USNM 588113	RP-PPIV	NU	N	4.5	3	1.5
USNM 588113	LM-IPIV	NU	N	4.5	2.5	1.8
USNM 269391	R-MCII	NU	Y	10	4	2.5
USNM 269391	R-MCIII	CO	Y	10.2	4.2	2.4285714
USNM 269391	R-MCIV	CO	Y	9.3	4.3	2.1627907
USNM 269391	R-MCV	CO	Y	9	4.3	2.0930233
USNM 269391	L-MCII	CO	Y	9.4	3.5	2.6857143
USNM 269391	L-MCIII	CO	CO	9.5	3	3.1666667
USNM 269391	L-MCIV	CO	Y	10.2	4.3	2.372093
USNM 269391	L-MCV	CO	Y	7.7	3.9	1.974359
USNM 269391	R-MTI	L	Y	2.8	1	2.8
USNM 269391	R-MTII	NU	Y	5.8	2.6	2.2307692
USNM 269391	R-MTIII	CO	CO	7	3	2.3333333
USNM 269391	R-MTIV	CO	CO	6.5	3.3	1.969697
USNM 269391	R-MTV	CO	CO	4.5	2.5	1.8
USNM 269391	L-MTI	CO	Y	3.2	1	3.2
USNM 269391	L-MTII	L	Y	6	2.6	2.3076923
USNM 269391	L-MTIII	CO	Y	7.9	3.8	2.0789474
USNM 269391	L-MTIV	CO	CO	6.3	2.9	2.1724138
USNM 269391	L-MTV	CO	Y	5	3	1.6666667
USNM 49639	R-MCI	NU	N	9	4	2.25
USNM 49639	R-MCII	L	N	15.5	5.5	2.8181818
USNM 49639	R-MCIII	L	N	16.9	6	2.8166667
USNM 49639	R-MCIV	NU	N	15	5	3
USNM 49639	R-MCV	L	N	14.3	5.5	2.6
USNM 49639	L-MCI	NU	N	9.5	3.9	2.4358974
USNM 49639	L-MCII	NU	N	15.2	5.2	2.9230769
USNM 49639	L-MCIII	L	N	16.3	5.8	2.8103448
USNM 49639	L-MCIV	U	N	15	5	3
USNM 49639	L-MCV	NU	N	12.5	5.5	2.2727273
USNM 49639	R-MTI	U	N	5	2.5	2
USNM 49639	R-MTII	L	N	9.5	4.2	2.2619048
USNM 49639	R-MTIII	U	N	11.6	5.3	2.1886792
USNM 49639	R-MTIV	U	N	10	4.2	2.3809524
USNM 49639	R-MTV	NU	N	7	5	1.4
USNM 49639	L-MTI	U	N	5.2	2.5	2.08
USNM 49639	L-MTII	L	N	9.5	4	2.375
USNM 49639	L-MTIII	U	N	12	5.7	2.1052632
USNM 49639	L-MTIV	L	Y	10.7	4.5	2.3777778
USNM 49639	L-MTV	NU	N	7.2	5.5	1.3090909
USNM 49489	R-MCI	NU	N	6.8	3	2.2666667
USNM 49489	R-MCII	L	N	12.8	5	2.56
USNM 49489	R-MCIII	L	N	15	5.5	2.7272727
USNM 49489	R-MCIV	L	N	13	5.8	2.2413793
USNM 49489	R-MCV	U	N	11.3	5.5	2.0545455
USNM 49489	R-MTII	CO	Y	8	4	2
USNM 49489	R-MTIII	U	N	10.5	4.5	2.3333333

USNM 49489	R-MTIV	U	N	9.2	4.1	2.2439024
USNM 49489	R-MTV	U	N	5.7	4.7	1.212766
USNM 20756	R-MCII	CO	Y	6.5	4	1.625
USNM 20756	R-MCIII	CO	Y	8.5	4.2	2.0238095
USNM 20756	R-MCIV	CO	Y	7.2	4.4	1.6363636
USNM 20756	R-MCV	CO	Y	5.5	2.8	1.9642857
USNM 20756	L-MCII	CO	Y	7.5	3.6	2.0833333
USNM 20756	L-MCIII	CO	Y	8	4.5	1.7777778
USNM 20756	L-MCIV	CO	Y	7	4.3	1.627907
USNM 20756	L-MCV	CO	Y	5.5	2.7	2.037037
USNM 20756	R-MTII	CO	Y	4.7	3	1.5666667
USNM 20756	R-MTIII	CO	Y	6.2	3.5	1.7714286
USNM 20756	R-MTIV	CO	Y	5.3	3.3	1.6060606
USNM 20756	R-MTV	CO	Y	3.5	2.2	1.5909091
USNM 20756	L-MTII	CO	Y	4.7	3	1.5666667
USNM 20756	L-MTIII	CO	Y	6	3.7	1.6216216
USNM 20756	L-MTIV	CO	Y	5.1	4	1.275
USNM 20756	L-MTV	CO	Y	3.3	2.1	1.5714286
USNM 266911	R-MCI	U	N	9.2	4	2.3
USNM 266911	R-MCII	U	N	14.5	4.9	2.9591837
USNM 266911	R-MCIII	U	N	17.3	6	2.8833333
USNM 266911	R-MCIV	U	N	15.5	5	3.1
USNM 266911	R-MCV	U	N	13.9	5	2.78
USNM 266911	R-MTII	U	N	10.5	3.7	2.8378378
USNM 266911	R-MTIII	U	N	11.5	4.5	2.5555556
USNM 266911	R-MTV	U	N	6.7	5	1.34
USNM 266911	L-MTIV	U	N	10.9	4	2.725
MSUMR no data	R-MCI	NU	N	7	2.6	2.6923077
MSUMR no data	R-MCV	NU	N	7.2	3.5	2.0571429
MSUMR no data	L-MCI	NU	N	7.7	2.7	2.8518519
MSUMR no data	L-MCV	NU	N	7.4	4.1	1.804878
MSUVP 1289	R-MCII	U	N	12.7	7.6	1.6710526
MSUVP 1289	L-MCI	U	N	8.2	4.9	1.6734694
MSUVP 1289	L-MCII	U	N	12	8.3	1.4457831
MSUVP 1289	R-MTIV	U	N	10.8	6.6	1.6363636
MSUVP 1289	RM-PPIV	NU	N	12.7	7.6	1.6710526
MSUVP 1289	LM-PPIII	NU	N	7.2	7.1	1.0140845
MSUMR 7550	R-MCII	U	N	18.8	6.5	2.8923077
MSUMR 7550	R-MCIII	U	N	20.1	7.7	2.6103896
MSUMR 7550	R-MCIV	U	N	18.3	8	2.2875
MSUMR 7550	R-MCV	L	N	15.1	6.6	2.2878788
MSUMR 7550	L-MCI	L	N	11.6	4.6	2.5217391
MSUMR 7550	L-MCII	U	N	17.5	9.5	1.8421053
MSUMR 7550	L-MCIII	U	N	19.9	7.8	2.5512821
MSUMR 7550	L-MCIV	U	N	18.2	7.6	2.3947368
MSUMR 7550	L-MCV	L	N	14.7	6.9	2.1304348
MSUMR 7550	R-MTI	N	N	7.2	2.9	2.4827586
MSUMR 7550	R-MTII	U	N	11.1	5	2.22
MSUMR 7550	R-MTIII	U	N	13.3	6	2.2166667
MSUMR 7550	R-MTIV	U	N	13.1	6.6	1.9848485

MSUMR 7550	R-MTV	U	N	8.4	5.8	1.4482759
MSUMR 7550	L-MTI	U	N	7	2.8	2.5
MSUMR 7550	L-MTII	L	N	11.5	5	2.3
MSUMR 7550	L-MTIII	U	N	14.1	6.2	2.2741935
MSUMR 7550	L-MTIV	U	N	13.7	6.6	2.0757576
MSUMR 7550	L-MTV	U	N	8.3	5.8	1.4310345
UMMZ no #	R-MCI	L	N	10	3.6	2.7777778
UMMZ no #	L-MCI	U	N	9.4	3.7	2.5405405
UMMZ no #	R-MCII	U	N	15.3	5.6	2.7321429
UMMZ no #	L-MCII	U	N	15.4	15.5	0.9935484
UMMZ no #	L-MCIII	U	N	15.9	6	2.65
UMMZ no #	L-MCIV	U	N	15.3	6.2	2.4677419
UMMZ no data	L-MTI	U	N	5.1	2.8	1.8214286
UMMZ no data	L-MTII	U	Y	10	4.9	2.0408163
UMMZ no data	L-MTIII	U	N	12	5	2.4
UMMZ no data	L-MTIV	U	N	10.9	4.9	2.2244898
UMMZ no data	L-MTV	U	N	7.5	5.4	1.3888889
UMMZ 157850	R-MCIII	U	CO	15.4	5.8	2.6551724
UMMZ 157850	L-MCI	U	N	8.6	3.2	2.6875
UMMZ 157850	L-MCII	U	Y	14.7	5.4	2.7222222
UMMZ 157850	L-MCV	U	CO	12.3	4.9	2.5102041
UMMZ 157850	R-MTI	NU	N	5.5	2.6	2.1153846
UMMZ 157850	R-MTII	U	N	9.8	4.4	2.2272727
UMMZ 157850	R-MTIII	U	N	10.5	5	2.1
UMMZ 157850	R-MTIV	U	N	9.4	4.8	1.9583333
UMMZ 157850	R-MTV	NU	N	6.8	6.3	1.0793651

Appendix B. Chi-square tests for significance.

ASU = articular surface undermining		
df = degrees of freedom		
o = observed		
e = expected		

Metapodials:

Metapodial	ASU	No ASU	Total		e (Yes)	e (No)
I	13	13	26		16.2303	9.769697
II	25	13	38		23.72121	14.27879
III	31	4	35		21.84848	13.15152
IV	26	6	32		19.97576	12.02424
V	8	26	34		21.22424	12.77576
Total	103	62	165			
Metapodial	Undermining	o	e	o-e	(o-e)^2/e	
I	Y	13	16.2303	-3.23030303	0.642924	
I	N	13	9.769697	3.23030303	1.068084	
II	Y	25	23.72121	1.27878788	0.068938	
II	N	13	14.27879	-1.27878788	0.114526	
III	Y	31	21.84848	9.15151515	3.833228	
III	N	4	13.15152	-9.15151515	6.368105	
IV	Y	26	19.97576	6.02424242	1.816777	
IV	N	6	12.02424	-6.02424242	3.018194	
V	Y	8	21.22424	-13.2242424	8.239662	
V	N	26	12.77576	13.2242424	13.68847	
df = (r-1)*(c-1) = 4				Chi-square	38.85891	

Metacarpals

Metacarpal	ASU	No ASU	Total		e (Yes)	e (No)
I	7	9	16		9.488372	6.511628
II	14	5	19		11.26744	7.732558
III	14	3	17		10.0814	6.918605
IV	13	2	15		8.895349	6.104651
V	3	16	19		11.26744	7.732558
Total	51	35	86			
Metacarpal	Undermining	o	e	o-e	(o-e)^2/e	
I	Y	7	9.488372	-2.48837209	0.652588	
I	N	9	6.511628	2.48837209	0.950914	
II	Y	14	11.26744	2.73255814	0.662695	
II	N	5	7.732558	-2.73255814	0.965641	
III	Y	14	10.0814	3.91860465	1.523149	
III	N	3	6.918605	-3.91860465	2.219445	
IV	Y	13	8.895349	4.10465116	1.894042	
IV	N	2	6.104651	-4.10465116	2.759889	
V	Y	3	11.26744	-8.26744186	6.066203	
V	N	16	7.732558	8.26744186	8.839325	
df = (r-1)*(c-1) = 4				Chi-square	26.53389	

Metatarsals

Metatarsal	ASU	No ASU	Total		e (yes)	e (no)
I	6	4	10		6.582278	3.417722
II	11	8	19		12.50633	6.493671
III	17	1	18		11.8481	6.151899
IV	13	4	17		2.797468	5.810127
V	5	10	15		9.873418	5.126582
Total	52	27	79			
Metatarsal	Undermining	o	e	o-e	(o-e)^2/e	
I	Y	6	6.582278	-0.58227848	0.051509	
I	N	4	3.417722	0.58227848	0.099203	
II	Y	11	12.50633	-1.50632911	0.18143	
II	N	8	6.493671	1.50632911	0.349421	
III	Y	17	11.8481	5.15189873	2.240195	
III	N	1	6.151899	-5.15189873	4.31445	
IV	Y	13	2.797468	10.2025316	37.20923	
IV	N	4	5.810127	-1.81012658	0.563939	
V	Y	5	9.873418	-4.87341772	2.405469	
V	N	10	5.126582	4.87341772	4.632755	
df = (r-1)*(c-1) = 4				Chi-square	52.04761	

Metacarpals II, III, and IV

Metacarpal	ASU	No ASU	Total		e (yes)	e (no)
II	14	5	19		15.27451	3.72549
III	14	3	17		13.66667	3.333333
IV	13	2	15		12.05882	2.941176
Total	41	10	51			
Metacarpal	Undermining	o	e	o-e	(o-e)^2/e	
II	Y	14	15.27451	-1.2745098	0.106345	
II	N	5	3.72549	1.2745098	0.436017	
III	Y	14	13.66667	0.33333333	0.00813	
III	N	3	3.333333	-0.33333333	0.033333	
IV	Y	13	12.05882	0.94117647	0.073458	
IV	N	2	2.941176	-0.94117647	0.301176	
df = (3-1)*(2-1) = 2				Chi-square	0.95846	

Metatarsals II, III, and IV

Metatarsal	ASU	No ASU	Total		e (yes)	e (no)
II	11	8	19		14.42593	4.574074
III	17	1	18		13.66667	4.333333
IV	13	4	17		12.90741	4.092593
Total	41	13	54			
Metatarsal	Undermining	o	e	o-e	(o-e)^2/e	
II	Y	11	14.42593	-3.42592593	0.813602	
II	N	8	4.574074	3.42592593	2.565977	
III	Y	17	13.66667	3.33333333	0.813008	
III	N	1	4.333333	-3.33333333	2.564103	
IV	Y	13	12.90741	0.09259259	0.000664	
IV	N	4	4.092593	-0.09259259	0.002095	
df = (3-1)*(2-1) = 2				Chi-square	6.759449	

REFERENCES

Abraczinskas, L.M. 1993. Pleistocene Proboscidean sites in Michigan: New records and an update on published sites. Michigan Academician 25:443-490.

Agenbroad, D. and Mead, J.I. 1996. Distribution and palaeoecology of central and western North American *Mammuthus*. In Shoshani, J., and Tassy, P. (eds.). The Proboscidea: Evolution and palaeoecology of elephants and their relatives. Oxford University Press, Oxford, 472 pp.

Andrews, C.W. 1906. A descriptive catalogue of the Tertiary Vertebrata of the Fayum, Egypt. London, British Museum, 319 pp.

Ayvazian, L.F. 1993. History of tuberculosis. In Reichman, L.B. and Hershfield, E.S. (eds.). Tuberculosis: A comprehensive international approach. New York, Marcel Dekker, 752 pp.

Binkley, M. 1997. Tuberculosis in captive elephants. Proceedings of the American Association of Zoo Veterinarians. Seattle, WA, p. 116-119.

Bricknell, I. 1987. Palaeopathology of Pleistocene proboscideans in Britain. Modern Geology 11:295-309.

Cope, E.D. 1887. The Perissodactyla. American Naturalist 21(11): 985-1007.

Douglas-Hamilton, I. And Michelmore, F. 1996. *Loxodonta africana*: range and distribution, past and present. Shoshani, J., and Tassy, P. (eds.). The Proboscidea: Evolution and palaeoecology of elephants and their relatives. Oxford University Press, Oxford, 472 pp.

Fisher, D.C. 1984. Taphonomic analysis of late Pleistocene mastodon occurrences: evidence of butchery by North American Paleo-Indians. Paleobiology 10:338-358.

Fischer, M.S. and Pascal Tassy. 1993. The interrelation between Proboscidea, Sirenia, Hyracoidea, and Mesaxonia: the morphological evidence. In Szalay, F.S., Novacek, M.J., and McKenna, M.C. (eds.). Mammal phylogeny: placentals, Springer-Verlage, New York, 1-321 pp.

Fowler, M.E. 2001. An overview of foot conditions in Asian and African elephants. In Csuti, B., Sargent, E.L., and Bechert, U.S. (eds.). The elephant's foot. Iowa State University Press, Ames, 163 pp.

Francis, J. 1958. Pathogenesis and Pathology. In Tuberculosis in animals and man: a study in comparative pathology. Cassell, London, 11-43.

Frothingham, R., Strickland, P.L., Bretzel, G., Ramasqamy, S., Musser, J.M., and

Williams, D.L. 1999. Phenotypic and genotypic characterization of *Mycobacterium africanum* Isolates from West Africa. Journal of Clinical Microbiology 37(6):1921-1926.

Gutter, A. 1981. *Mycobacterium tuberculosis* in an Asian elephant. Proceedings of the American Association of Zoo Veterinarians. Seattle, WA., p. 105-106.

Hildebrand, M. and Hurley, J.P. 1985. Energy of the oscillating legs of a fast-moving cheetah, pronghorn, jackrabbit, and elephant. Journal of Morphology 184:23-31.

Hildebrand, M. 1976. Analysis of tetrapod gaits: general considerations and symmetrical gaits. In R.M. Herman et al. (eds.). Neural Control of Locomotion. Advances in Behavioral Biology, 18. New York, Plenum Press.

Holman, J.A. 1975. Michigan's Fossil Vertebrates. Stone Printing Company, Lansing, Michigan, 54 pp.

Holman, J.A. 1995. Ancient life of the Great Lakes Basin: Precambrian to Pleistocene. University of Michigan Press, Ann Arbor, Michigan, 287 pp.

Holman, J.A., Fisher, D.C., and Kapp, R.O. 1986. Recent discoveries of fossil vertebrates in the Lower Peninsula of Michigan. Michigan Academician 28(3):431-463.

Hoop, R.K. 2002. *Mycobacterium tuberculosis* infection in a canary (*Serinus canaria L.*) and a Blue-Fronted Amazon Parrot (*Amazona amazona aestiva*). Avian Diseases 46:502-504.

Hoop, R.K., Böttger, E.C., and Pfyffer, G.E. 1996. Etiological agents of mycobacterioses in pet birds between 1986 and 1995. Journal of Clinical Microbiology 34:991-992.

King, J.E. and Saunders, J.J. 1984. Environmental Insularity and the Extinction of the American mastodont. In Martin, P.S. and Klein, R.G (eds.). Quaternary Extinctions. University of Arizona Press, Tuscon, 315-339.

Klaits, B.G. 1972. The moving mesaxonic manus: a comparison of tapirs and rhinoceroses. Mammalia 36(1):126-145.

Lomme, J.R., et al. 1976. *Mycobacterium tuberculosis* infection in two East African oryxes. Journal of the American Veterinary Medical Association 169(9):912-914.

Maglio, V.J. 1972. Evolution of Mastication in the Elephantidae. Evolution 26:638-658.

Marsh, O.C. 1884. Dinocerata, a monograph of an extinct order of gigantic mammals. U.S. Geological Survey Monography 10 (28):1-237.

Meghji, S., White, P.A., Nair, S.P., Reddi, K., Heron, K., Henderson, B., Zalianai, A., Fossati, G., Mascagni, P., Hunt, J.F., Roberts, M.M. and Coates, A.R.M. 1997. *Mycobacterium tuberculosis* Chaperonin 10 stimulates bone resorption: a potential contributory factor in Pott's Disease. Journal of Experimental Medicine 186(8):1241-1246.

Michel, A.L. 2002. Implications of tuberculosis in African wildlife and livestock. Annals of the New York Academy of Sciences 969:251-255.

Mikota, S.K., Larsen, R.S., and Montali, R.J. 2000. Tuberculosis in elephants in North America. Zoo Biology 19:393-403.

Mikota, S.K., Peddie, L., Peddie, J., Isaza, R., Dunker, R., West, G., Lindsay, W., Larsen, R.S., Salman, M.D., Chatterjee, D., Payeur, J., Whipple, D., Thoen, C., Davis, D.S., Sedgwick, C., Montali, R.J., Ziccardi, M., and Maslow, J. 2001. Epidemiology and diagnosis of *Mycobacterium tuberculosis* in captive Asian elephants (*Elephas maximus*). Journal of Zoo and Wildlife Medicine 32(1):1-16.

Montali, R.J., Bush, M., Thoen, C.O., and Smith, E. 1976. Tuberculosis in captive exotic birds. Journal of the American Veterinary Medical Association 169:920-927.

Nair, S.P., Meghji, S., Wilson, M., Reddi, K., White, P., and Henderson, B. 1996. Bacterially induced bone destruction: mechanisms and misconceptions. Infection and Immunity 64: 2371-2380.

Payeur, J.B., J.L. Jarnagin, J.G. Marquardt, and D.L. Whipple. 2002. Mycobacterial isolations in captive elephants in the United States. Annals of the New York Academy of Sciences 969:256-258.

Powers, R.D. and Price, R.A. 1967. Human tuberculosis in a rhinoceros. Journal of the American Veterinary Medical Association 151(7):890-892.

Ramsay, E.C. and Henry, R.W. 2001. Anatomy of the elephant foot. In Csuti, B., Sargent, E.L., and Bechert, U.S. (eds.). The elephant's foot. Iowa State University Press, Ames, 163 pp.

Richman, L.K., R.J. Montali, R.C. Cambre, J. Lehnhardt, M. Kennedy, S. Kania, and L. Potgieter. 1996. Endothelial inclusion body disease: a newly recognized fatal herpes-like infection in Asian elephants. Proceedings of the American Association of Zoo Veterinarians 1996:483-485.

Roocroft, A. and Oosterhuis, J. 2001. Foot care for captive elephants. In Csuti, B., Sargent, E.L., and Bechert, U.S. (eds.). The elephant's foot. Iowa State University Press, Ames, 163 pp.

Rothschild, B.M. 1988. Stress fracture in a ceratopsian phalanx. Journal of Paleontology 62(2):302-303.

Rothschild, B. and Helbling, M. 2001. Documentation of hyperdisease in the Late Pleistocene: validation of an early 20th century hypothesis. Journal of Vertebrate Paleontology, Abstracts of Papers 21(3):94A.

Rothschild, B.M. and Martin, L. (eds.). 1993. Paleopathology: disease in the fossil record. CRC Press, London, England, 361 pp.

Rothschild, B.M., Martin, L.D., Lec, G. Bercovier, H., Bar-Gar, G.K., Greenblatt, C., Donoghue, H., Spigelman, M., and Brittain, D. 2001. *Mycobacterium tuberculosis* complex DNA from an extinct bison dated 17,000 years before the present. Clinical Infectious Diseases 33:305-11.

Rothschild, B.M., Xiaoming, W., and Shoshani, J. 1994. Spondyloarthropathy in proboscideans. Journal of Zoo and Wildlife Medicine 25:360-366.

Sadler, W.C. 2001. The role of nutrition and its possible impact on elephant foot care. In Csuti, B., Sargent, E.L., and Bechert, U.S. (eds.). The elephant's foot. Iowa State University Press, Ames, 163 pp.

Saunders, G. 1983. Pulmonary *Mycobacterium tuberculosis* infection in a circus elephant. Journal of the American Veterinary Medical Association 183(11):1311-1312.

Saunders, J.J. 1996. North American Mammutidae. In Shoshani, J., and Tassy, P. (eds.). The Proboscidea: Evolution and palaeoecology of elephants and their relatives. Oxford University Press, Oxford, 472 pp.

Schultz, C.B. 1963. Fossil hunting yesterday and today. Museum Notes 22:18.

Shoshani, J. 1989. A report on the Shelton mastodon site and a discussion of the numbers of mastodons and mammoths in Michigan. Michigan Academician 21(2):115-132

Shoshani, J. 1992. Comparing the living elephants. In Shoshani, J. (ed.). Elephants: Majestic creatures of the wild. Rodale Press, Inc., Pennsylvania, 240 pp.

Shoshani, J. 1996. Skeletal and other basic anatomical features of elephants. In Shoshani, J., and Tassy, P. (eds.). The Proboscidea: Evolution and palaeoecology

of elephants and their relatives. Oxford University Press, Oxford, 472 pp.

Shoshani, J. and Tassy, P. 1996. Summary, conclusions, and a glimpse into the future. In Shoshani, J., and Tassy, P. (eds.). The Proboscidea: Evolution and palaeoecology of elephants and their relatives. Oxford University Press, Oxford, 472 pp.

Skeels, M.A. 1962. The mastodons and mammoths of Michigan. Papers of the Michigan Academy of Science, Arts, and Letters 1:103-33.

Smuts, M.M.S. and Bezuidenhout, A.J. 1993. Osteology of the thoracic limb of the African elephant (*Loxodonta africana*). Onderstepoort Journal of Vet. Res. 60:1-14.

Sreevatsan, S., Pan, X., Stockbauer, K.E., Connell, N.D., Kreiswirth, B.N., Whittam, T.S., and Musser, J.M. 1997. Restricted structural gene polymorphism in the Mycobacterium tuberculosis complex indicates evolutionarily recent global dissemination. Proceedings of the National Academy of Sciences 94:9869-9874.

Sukumar, R. and Santiapillai, C. 1996. *Elephas maximus*: status and distribution. In Shoshani, J., and Tassy, P. (eds.). The Proboscidea: Evolution and palaeoecology of elephants and their relatives. Oxford University Press, Oxford, 472 pp.

Tassy, P. 1996. Who is who among the Proboscidea? In Shoshani, J., and Tassy, P. (eds.). The Proboscidea: Evolution and palaeoecology of elephants and their relatives. Oxford University Press, Oxford, 472 pp.

Tassy, P. and Shoshani, J. 1988. The Tethytheria: elephants and their relatives. In Benton, M.J. (ed.). The phylogeny and classification of the tetrapods, volume 2: Mammals. Clarendon Press, Oxford, 344 pp.

Taylor, G.M., Goyal, M., Legge, A.J., Shaw, R.J., and Young, D. 1999. Genotypic analysis of *Mycobacterium tuberculosis* from medieval human remains. Microbiology 145:899-904.

Thewissen, J.G.M. and Domning, D.P. 1992. The role of phenacodentids in the origin of the modern orders of ungulate mammals. Journal of Vertebrate Paleontology 12(4):494-504.

Thomas, M.G., Hagelberg, E., Jones, H.B., Yang, Z., and Lister, A.M. 2000. Molecular and morphological evidence on the phylogeny of Elephantidae. Proceedings of the Royal Society of London (Series B) 267:2493-2450.

Urbain, A. 1938. L'infection tuberculeuse spontanee chez les mammiferes sauvages en

captivite. American Institute Pasteur 61:705-730.