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MAMMUT AMERICANUM (KERR, 1792)

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Fossil Species of Florida is a publication of the Florida Paleontological Society, Inc. (FPS), and is intended to provide basic information about common or important fossil species found in the state. For vertebrates, it will supplement information provided in the book *The Fossil Vertebrates of Florida* published by the University Press of Florida for the FPS in 2001. It is anticipated that several issues will be produced each year. The earlier issues in the series will primarily cover vertebrate species, but eventually it will encompass all taxonomic groups and include articles on fossil plants, invertebrate animals, and microfossils. Planned forthcoming issues will be on the tapir *Tapirus veroensis*, the rhino *Aphelops mutilus*, and the tortoise *Hesperotestudo incisa*. The editor of *Fossil Species of Florida* is Dr. Richard C. Hulbert, Vertebrate Paleontology Collections Manager, Florida Museum of Natural History, Dickinson Hall, Gainesville (e-mail: rhulbert@flmnh.ufl.edu). Contact Dr. Hulbert for suggestions as to species we should cover or if you are interested in authoring an article in the series. Do not submit unsolicited manuscripts.

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The American mastodon belongs to the group of mammals known as proboscideans, which consists of the living elephants and their extinct relatives. Like other proboscideans, the American mastodon is characterized by very large size, pillar-like legs, a manipulative proboscis (the trunk), and protruding tusks.

Proboscideans today consist of only two genera–*Loxodonta* (the African elephant) and *Elephas* (the Indian elephant). But the fossil record preserves an impressive history of a much more diverse and wide-spread group. The most primitive proboscideans lived in southern Asia and northern Africa during the Eocene Epoch about 40 to 50 Ma[1]. The mastodon family Mammutidae evolved in Africa and spread through the Old World about 20 Ma. It was not until the middle Miocene (15 Ma), however, that mastodons first entered North America. Three species of mastodons are known from Florida–*Zygolophodon tapiroides*, from the middle Miocene (about 12 Ma); *Mammut sellardsi*, from the early Pliocene (about 5 Ma); and *Mammut americanum* from the late Pliocene (2.5 Ma) and Pleistocene.

Descriptions of bones and teeth of *Mammut americanum* date back as early as 1705, making this animal one the earliest fossils reported from North America (Miller 1987). The mastodon was even a great favorite of Thomas Jefferson, who believed that the mastodon and ground sloths still lived in the "West" and instructed Lewis and Clark to learn more about them (King and Saunders 1984). A wealth of information and findings on this species have been published over the last three centuries.

Several complete or nearly complete skeletons of the American mastodon have been recovered from Florida, including individuals on display at the Florida Museum of Natural History in Gainesville (Fig. 1) and the Museum of Florida History in Tallahassee. Partial jaws, isolated teeth, tooth fragments, broken tusks, limb bones, and vertebrae are the most common fossils of this species, and are most frequently found in riverbed deposits (Hulbert 2001).

VERTEBRATA
TETRAPODA
MAMMALIA
TETHYTHERIA
PROBOSCIDEA
MAMMUTIDAE
MAMMUT AMERICANUM

Taxonomic History—Cotton Mather discovered the first American mastodon fossils in 1705 in Albany, New York (Miller 1987), but it was not until 1792 that Robert Kerr first gave the fossils a formal scientific name, *Elephas americanus*. In 1806, the renowned French anatomist Georges Cuvier designated the genus *Mastodon* and replaced Kerr's species name (*americanum*) with *Mastodon giganteus*. But the genus name *Mammut* was earlier coined in 1799 by Blumenbach. It was not until the mid-1900s that *Mammut* was generally accepted by the scientific community and replaced *Mastodon* as the genus for Kerr's species. Today, the accepted Linnaean

[1] Ma = millions of years ago.

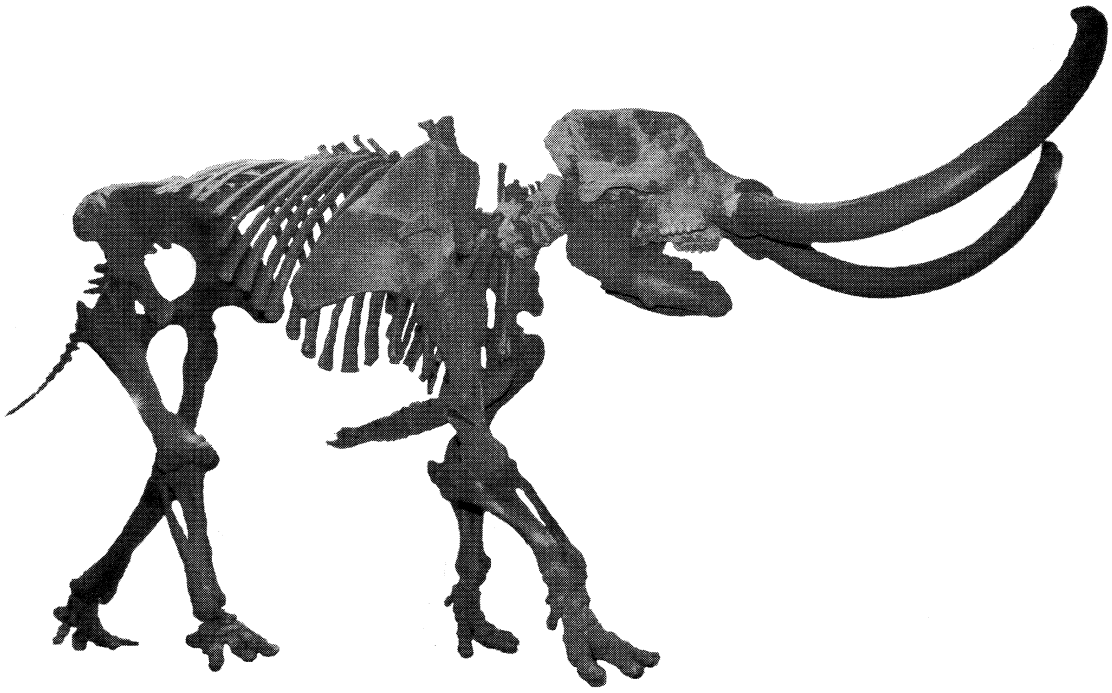

FIGURE 1. Mounted skeleton of an American mastodon (*Mammut americanum*) from the Aucilla River, Taylor-Jefferson county line, Florida. This specimen (UF 211300) is on display at the Florida Museum of Natural History. Photo by Jeff Gage; © Florida Museum of Natural History.

binomial name for the American mastodon is *Mammut americanum*.

Although paleontologists currently recognize only one valid species of North American mastodon during the late Pliocene and Pleistocene, this was not always the case (Osborn 1942, Miller 1987). During the 1800's and 1900's, subtle differences in size, tooth and tusk features, and the shape of the mandible and skull were used to erect over 20 different species of mastodons. These anatomical differences are now interpreted as the result of normal variation in a single species resulting from differences between males and females and between populations living in different habitats and climate.

Chronologic Range—*Mammut americanum* lived during the late Pliocene and Pleistocene. The oldest American mastodon fossils discovered so far have been dated to 3.75 Ma (from the White Bluffs in South Central Washington). However, the oldest fossil of *M. americanum* from Florida is about 2 Ma. The species became extinct about 10 to 11 thousand years ago.

Geographic Range—The American mastodon ranged widely throughout North America and is known from interior Alaska to central Mexico. A close relative, *Mammut borsoni*, is known from Asia and Europe. Mastodon remains are more common in the eastern United States than in the west. In Florida specifically, it has been found at numerous localities around the entire state (Fig. 2).

Key Florida Specimens[2]—Late Pliocene: Inglis 1A, Citrus County: UF 18119, lower right third molar. Santa Fe 1B, Columbia County: UF 144175, mandible with second and third molars (oldest records of mastodon in Florida).

Early Pleistocene: Leisey Shell Pit 1A, Hillsborough County: UF 81513, adult lower tusk; UF 81453, right mandible with last

[2] UF = Florida Museum of Natural History, vertebrate paleontology collection catalogue number.

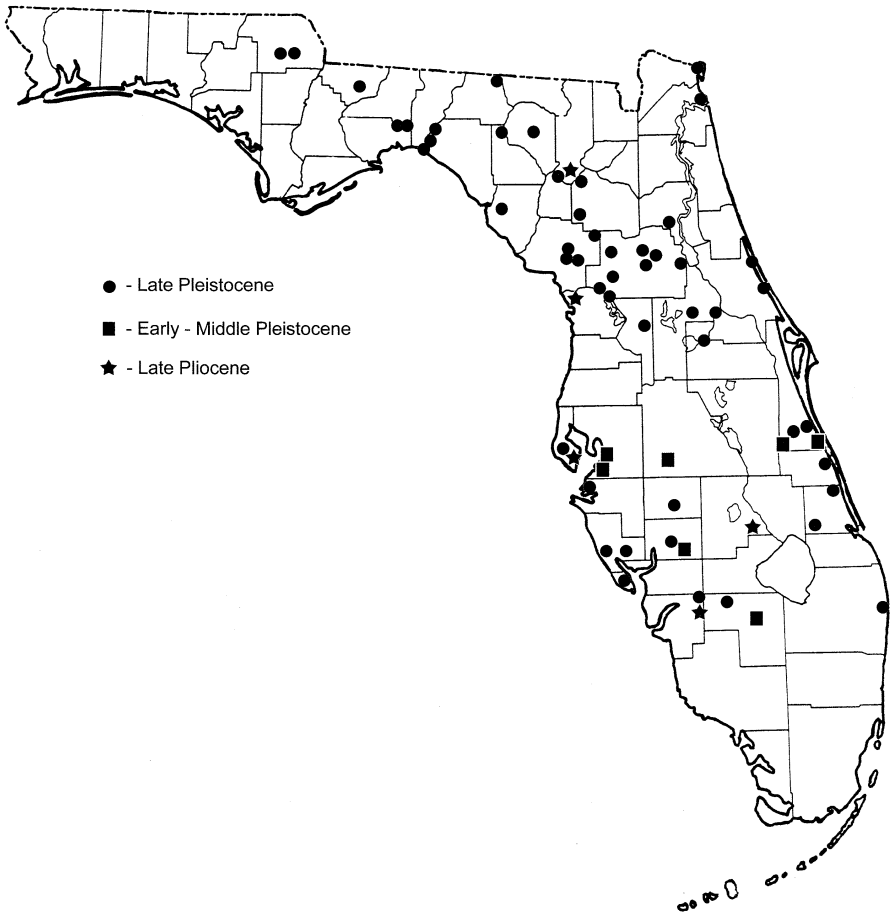

FIGURE 2. Map of Florida localities (with ages) where American mastodon remains have been found, based on UF and Florida Geological Survey collections at the Florida Museum of Natural History.

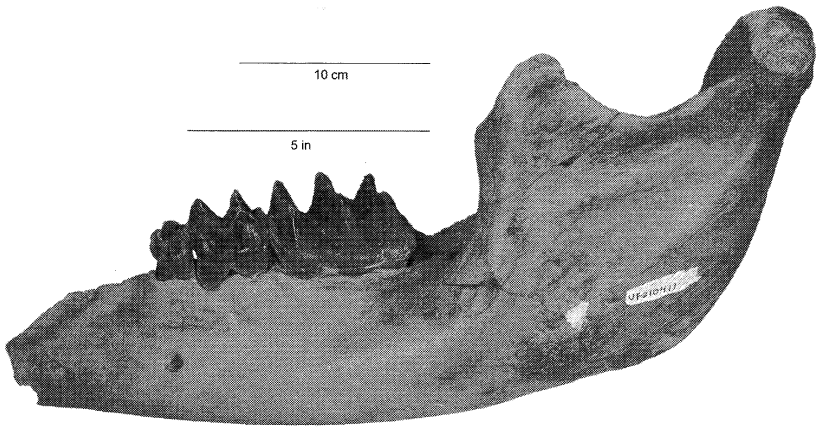

FIGURE 3. Left mandible of a juvenile *Mammut americanum*, UF 210411, with three deciduous premolars. The first two deciduous premolars have two lophs, while the last has three lophs. Specimen is from Hendry County, Florida.

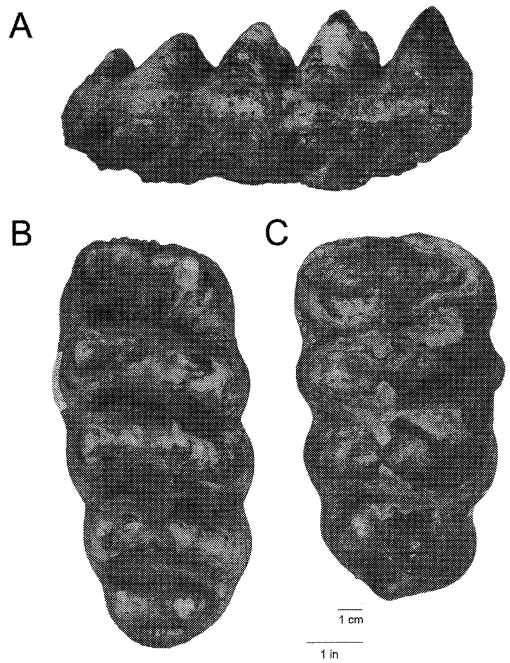

FIGURE 4. *Mammut americanum* third molars. **A**, Side view of lower third molar, UF 135717. **B**, Lower right third molar, UF 135717, with the lophs slanted. **C**, Upper right third molar, UF 135724, with the lophs at right angles to the long axis of the tooth. Specimens are from the Aucilla River, Florida.

deciduous premolar and first molar.

Middle Pleistocene: Tri-Britton Site, Hendry County: UF 210450, left mandible with third molar; UF 206854, left maxilla with first two molars; UF 210411, left mandible with deciduous premolars and first molar.

Late Pleistocene: Surprise Cave, Alachua County: UF 160000, skeleton (infant). Ichetucknee River, Columbia County: UF 32309, left mandible with third molar. West Palm Beach, Palm Beach County: UF 18505, skull; UF 18504, mandible with second and third molars. Wakulla Springs, Wakulla County: uncatalogued specimen, skeleton (adult), on display at Museum of Florida History in Tallahassee. Wekiwa River, Seminole County: UF 135586, partial skeleton with tusks. Aucilla River, Taylor County: UF 137891, skeleton (adult); UF 24126, skull; UF 211300, skeleton (adult), on display at Florida Museum of Natural History in Gainesville.

MORPHOLOGY

Skull—Generally, the mastodon skull is low and long, with the mandible being shallow and possessing an short symphysis with alveoli from which the small lower tusks protrude. The upper tusks were large and extend from alveoli at the anterior end of the skull. The skull itself has been modified to reduce weight by adding numerous air passages and sinuses to the bone in the skull roof. Fossil bone chunks possessing these air cavities are commonly found and are representative of this modification. Compared to mammoths, the other common Pleistocene proboscidean in Florida, the mastodon skull was longer, wider, and does not bear the domed head so prominent in mammoths.

Dentition—The cheek teeth of proboscideans are built on a basic pattern of transverse ridges known as lophs. In their lifetime, mastodons use six cheek teeth per jaw quadrant—three deciduous premolars (the equivalent of milk teeth; Fig. 3) and three molars. The first two premolars have only two lophs, while the last premolar and the first and second molars have three. Although similar in shape, size can be used to distinguish the latter three teeth. Last premolars average about 2.8 inches in length by 2.2 inches in width; first molars average 3.4 inches by 2.8 inches; and second molars 4.5 inches by 3.3 inches. The third and last molar has at least four lophs with five or more possible, making this tooth the longest in the series of cheek teeth (Fig. 4A). Complete specimens have an average length of about 6.9 inches and width of about 3.7 inches. One noteworthy third molar from the Aucilla River, Taylor County (UF 135718) is a very long 8.5 inches.

Mastodon upper and lower cheek teeth can be distinguished by comparing the trends of the cross-lophs. In the uppers, the lophs cross the long axis of the tooth at a right angle, whereas in the lowers they are slanted (Fig. 4B-C). In the orientation of the upper and lower jaws, the mandibular teeth con-

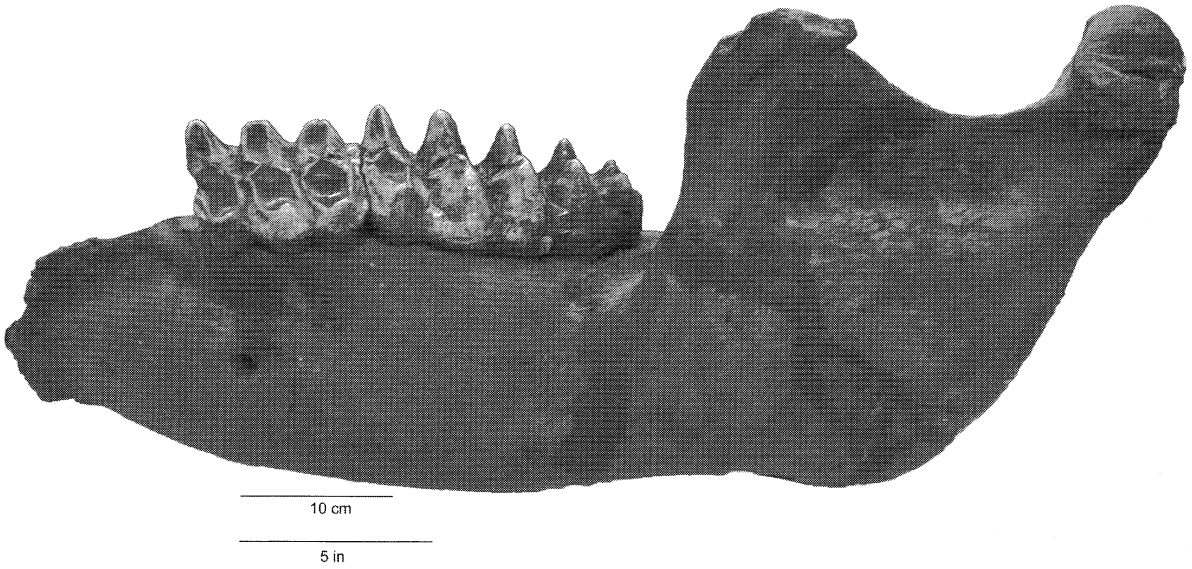

FIGURE 5. Left adult mandible of *Mammut americanum*, UF 18504, with second and third molars. Specimen is from Palm Beach County, Florida.

verge slightly anteriorly. The upper teeth diverge anteriorly, however, so that when the jaws are closed the lophs of each tooth fit into the interloph valleys of the opposing tooth (Laub 1996).

Mastodons, like other proboscideans, erupt cheek teeth horizontally instead of vertically, much like a conveyor belt. In vertical tooth succession found in most mammals, including humans, the worn out deciduous cheek teeth are replaced by permanent teeth that form either above or below them. However, in horizontal succession, as teeth wear down and become useless, they are pushed forward out of the mouth from behind by the less worn, younger teeth.

The tooth succession in mastodons, and other proboscideans, proceeds as follows. At birth, the animal has two deciduous premolars in each jaw quadrant. The final premolar erupts behind these two. The first and second molars erupt sequentially next, pushing the premolars forward. By the time second molar has completely erupted and is in use, the first and second premolars are lost. This is the young adult stage of a mastodon's life, where three teeth (the last premolar, and first and second molars) are present in the jaw. As the third molar erupts from the rear of the jaw, the last premolar is pushed out, and by the time this molar has completely erupted, the first molar is shed as well. This is the mature adult stage, where tooth eruption finally stops, leaving only the second and third molars in the jaw (Fig. 5). Finally, the second molar is lost in the very late phase of life, leaving only the third molar (Hulbert 2001).

The tusks are also part of the dentition in proboscideans, as they are enlarged, evergrowing incisors. All other incisors and the canines were lost early in proboscidean evolution. The tusk mainly consists of laminated rings or sheets of ivory, a type of dentine. The primitive number of tusks is four, with two uppers and two lowers. The short, cylindrical lower tusks tend to be much smaller and shorter than the uppers (Fig. 6). The presence or absence of lower tusks in adult American mastodons and their size, if present, is highly variable. In geologically older populations, lower tusks tend to be larger and occur more frequently. Also, lower tusks may be more common in males than females, especially in Pleistocene samples (Laub 1999).

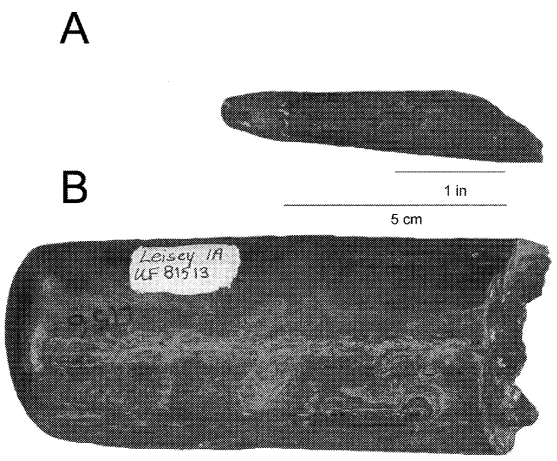

FIGURE 6. Lower tusks from *Mammut americanum*. **A**, Juvenile lower tusk, UF 86889. **B**, Adult lower tusk, UF 81513. Specimens are from Hillsborough County, Florida.

Postcranial Skeleton—Due to the massive size of the species, skeletal elements tend to quite large (Fig. 7). The limb bones are heavy and massive, with the humerus and femur usually being at least three to four feet long in mature adults. The ulna is more heavily developed than the radius at its distal end and supports most of the forearm weight. In the hind legs, the fibula is separate from the tibia and possesses a greatly expanded and flattened distal end. Dorsally and ventrally flattened carpal and tarsal bones are characteristic of the feet, which have five digits. These digits surround a dense heel pad, which help transmit the animal's weight to the ground. Both hind and fore feet to be short and broad, with the hind foot being narrower. The pelvis is fan-shaped, with the pubis and ischium being short and stout. The scapula has a long, flat cranial angle. The cervical vertebrae are compressed and appear very short when viewed laterally, with a dorsally rounded vertebral foramen. The thoracic vertebrae exhibit strong, high neural spines, while the lumbar vertebrae have heavily built centra and short, stout neural spines (Fig. 8). The sacral vertebrae are sometimes fused to form a solid unit, and nothing diagnostic is noted about the caudal vertebrae. The atlas is an uncomplicated, flattened ring of bone with a pronounced ventral tubercle and a curved dorsal margin. The axis has a high, pronounced neural spine with a well-defined odontoid process present (Olsen 1972).

Keys to Specific Identification—Because the American mastodon was the only mastodon that existed during the late Pliocene-Pleistocene in Florida, any mastodon fossils from this time interval can be inferred to be from *Mammut americanum*.

All six *M. americanum* teeth have distinct, ridge-like lophs and number from either two to five or six and increase in size in succession. The rigid lophs of the mastodon tooth are easily distinguished from the plate-like dentition of mammoth teeth. Gomphothere teeth also have lophs, but they are more numerous than the mastodon tooth and more rounded, rather than ridge-like (Fig. 9). Only when wear on gomphothere teeth becomes so excessive that the loph pattern is obliterated are they mistaken for mastodon teeth.

If the geologic context and age of the fossils in unknown, identification of the American mastodon to the species level can be rather difficult in terms of dentition. In terms of identifying *Mammut americanum* teeth compared to the two other mastodonts from Florida, *Zygolophodon* teeth are slightly narrower and lower crowned with small accessory cusps. *Mammut sellardsi* also had narrower teeth than its late Pliocene-Pleistocene relative.

Although tusks of mammoths and mastodons are compositionally the same, differences in the way the upper tusks leave the skull are clear. In the mastodon, the tusks project more or less horizontally from the skull, curving at first outward and later inward. Mammoth tusks, however, leave the skull nearly vertically, curve downward and outward, then begin the curve that brings the tips inward to each other. A mastodon usually has one tusk longer than the other, with

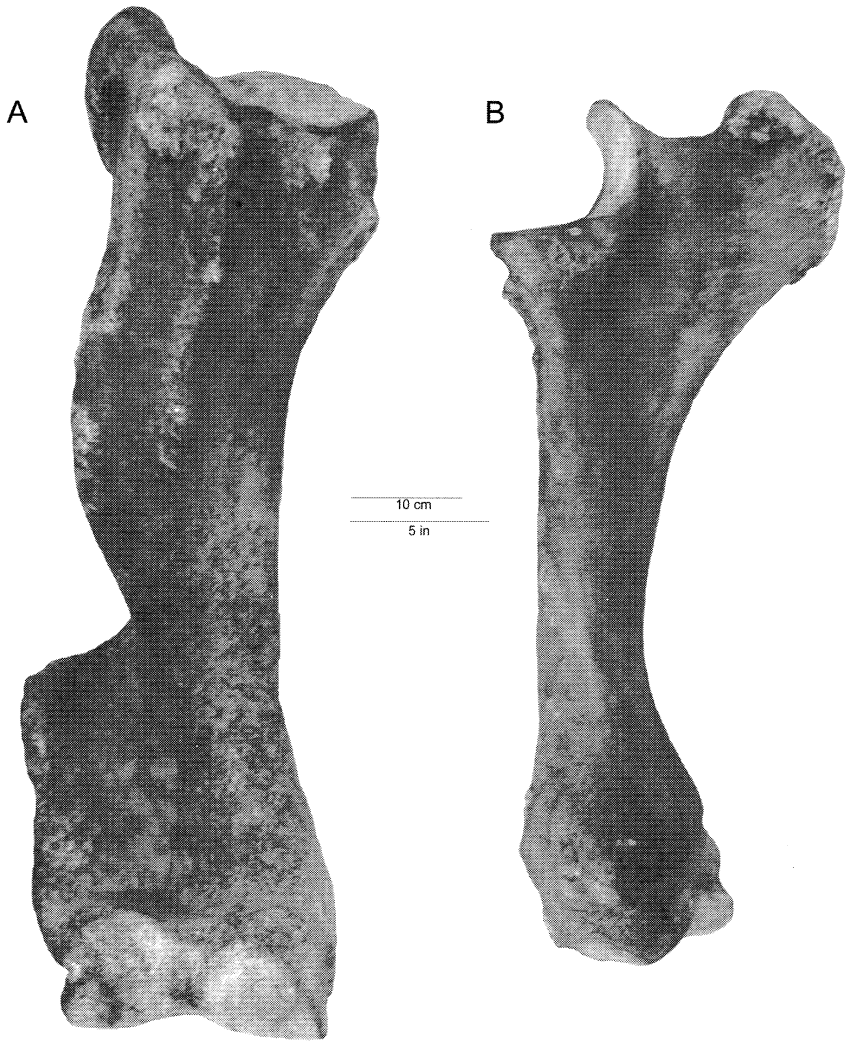

FIGURE 7. **A**, humerus, and **B**, ulna, of *Mammut americanum*, UF 137891, Taylor County, Florida.

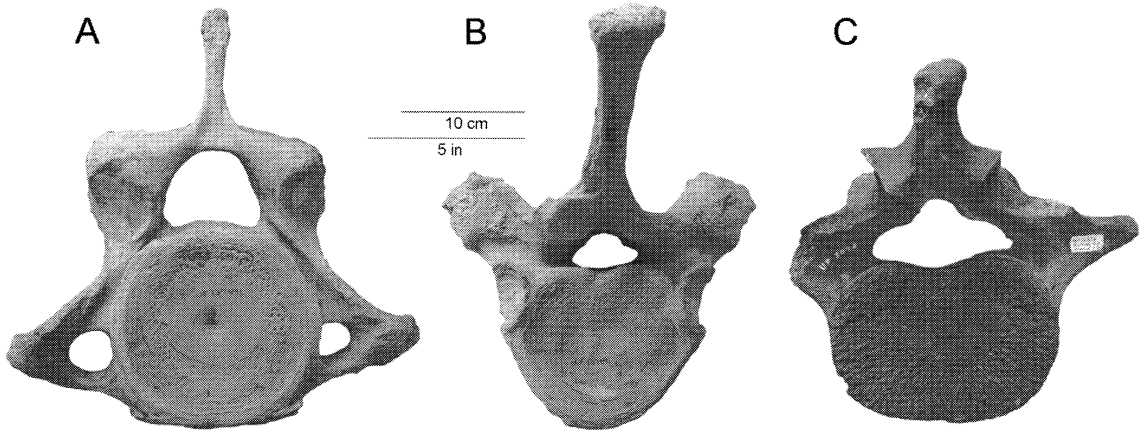

FIGURE 8. **A**, *Mammut americanum* cervical vertebrae, UF 137891, Taylor County, Florida; **B**, *M. americanum* thoracic vertebrae, UF 137891, Taylor County, Florida; **C**, *M. americanum* lumbar vertebrae, UF 3896, Alachua County, Florida.

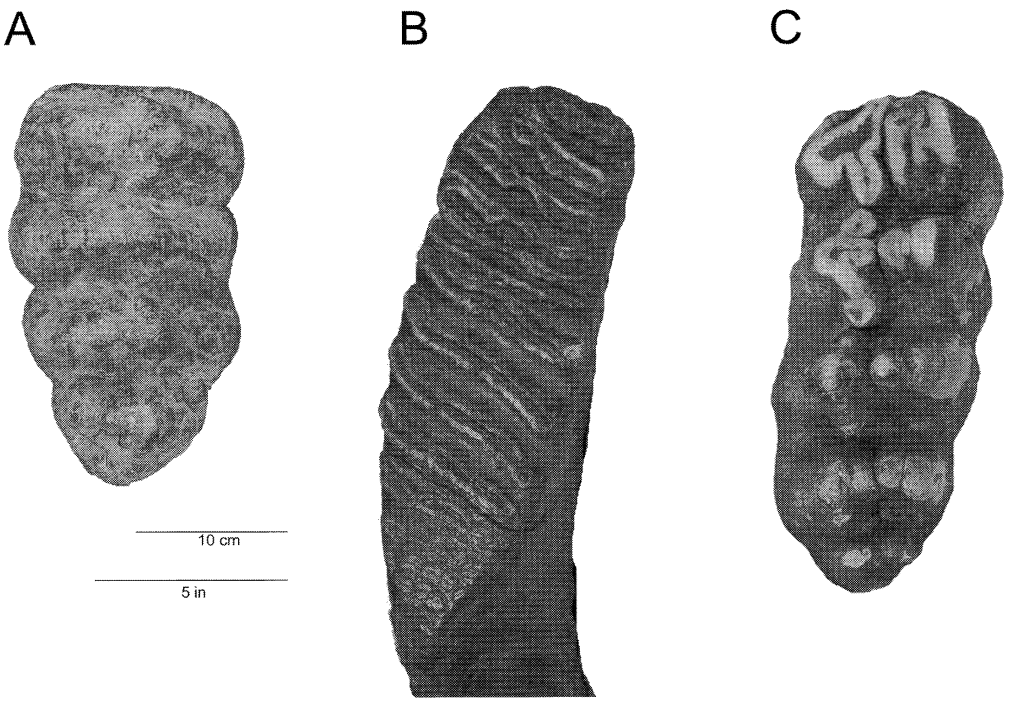

FIGURE 9. Florida mastodon, mammoth, and gomphothere molar comparison. **A**, Mastodon (*Mammut americanum*) molar, UF 135723. **B**, Mammoth (*Mammuthus columbi*), UF 135733. **C**, Gomphothere (*Cuvieronius tropicus*) molar, Daytona Museum of Arts and Sciences 695.

FIGURE 10. Front view of *Mammut americanum* skull, UF 211300, showing much greater wear and polishing on left tusk than right tusk, indicating preferred use of the left tusk by this individual. Some mastodons, like this one, were "left-tusked", while others were "right-tusked." Photo by Jeff Gage; © Florida Museum of Natural History.

the shorter tusk showing breakage and polish at the tip, indicating actual use of the tusks (Fig. 10). Mammoth tusks, however, do not show any wear or sign of use at all (Skeels 1962).

Postcranial elements of all proboscideans are similar, although some minor morphological differences exist. However, these can only be distinguished by direct association with cranial remains or by careful comparative analysis. (Hulbert 2001). Dentition is probably the most reliable and effective tool for identifying *M. americanum* down to the species level.

Paleoecology—The American mastodon was primarily a forest animal, browsing mainly on trees and shrubs (leaves, pine needles, bark, twigs, fruit, etc.) rather than coarse vegetation like grass. Actual remains of masticated vegetable matter have been found containing broken twigs from coniferous trees and leaves. Specifically, Webb et al. (1992) reported mastodon digesta from the Aucilla River of Florida consisting of small, broken woody pieces. The tusks are thought to aid in feeding, with the animal using a particular tusk to pry off and break apart the branches and trees they fed on. As with modern day elephants, only one tusk is used in this operation, indicating that the animal was either "right" or "left-tusked." This accounts for the wear shown on only one tusk in a pair rather than both, as indicated earlier (Skeels 1962).

At least some mastodon populations were migratory. Using strontium isotope ratios from tooth enamel, Hoppe et al. (1999) found that late Pleistocene individuals from northern and central Florida appear to have migrated north into central Georgia, over distances of 75 to 185 miles. Mastodons appear to have been nomadic migrants, rather than seasonal migrants, however. Thus, habitat and food source changes may account for such migratory behavior.

Extinction—Much controversy and debate surround the extinction of the American mastodon, as well as other megafauna from the late Pleistocene. To date, several theories have been proposed, from the extinction being caused by overkill by Paleo-Indians to dramatic climate and habitat change about 10,000 years ago.

American mastodon and Paleoindian Interactions—The interaction between Paleoindians and late Pleistocene megafauna is a popular topic in archaeology and paleontology. As the Paleoindians moved into North America, they came into contact with numerous small herds of *M. americanum*, thus providing the opportunity for hunting and butchery to take place. Mastodon butchery has been inferred primarily from patterns of bone modification, such as the production and use of tools fashioned from these bones (Fig. 11). Also, cut-marks and burned bone are indicators of human predation on mastodons. Paleoindian artifacts made from proboscidean ivory, butchered bone, and the association of hunting knives in close proximity to mastodon fossils have been discovered. A bone projectile point found embedded in a mastodon rib is also direct evidence of hunting by early man (Gustafson et al. 1979).

Several records of Paleoindian and mastodon interaction are recorded from Florida. The Aucilla River Prehistory Project (ARPP) was created in 1994 by the Florida Museum of Natural History to study the co-existence of early Floridians and Pleistocene megafauna. Since 1960, an Aucilla site known as Sloth Hole has yielded numerous ivory artifacts (Fig. 11). Of particular interest, a juvenile *M. americanum* fibula with two parallel "cut-marks" was recovered, along with a bifacial preform cutting tool and hammerstone with five battered surfaces, all in close proximity. Such data indicates a probable mastodon butchery site (Hemmings 1998).

This evidence supports the hypothesis that "overkill" was a contributing factor to the extinction of the American mastodon. Such extinction is produced by an "intense but

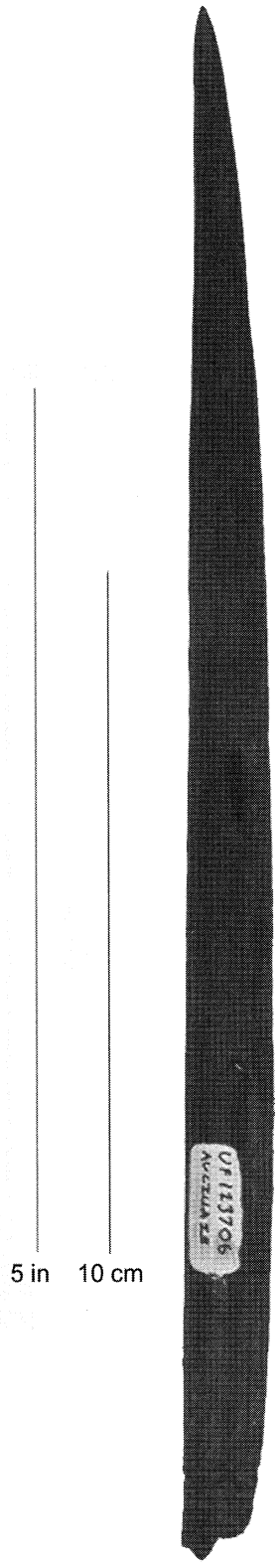

FIGURE 11. Spear point made of *Mammut americanum* ivory, from Sloth Hole, Aucilla River, UF 123706, Taylor County, Florida.

locally brief period of hunting, associated with a rapidly expanding front of human population density moving through North America" (Fisher 1984:339).

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