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TAPHONOMY OF THE LARGE VERTEBRATE FAUNA FROM THE THOMAS FARM LOCALITY (MIOCENE, HEMINGFORDIAN), GILCHRIST COUNTY, FLORIDA

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RESUMEN

Se presentan los resultados de una investigación tafonómica en la localidad de Thomas Farm. La evidencia sedimentológica indica que la deposición ocurrió en un cenote grande (alrededor de 35 m de diámetro), y profundo (30 m). Los sedimentos fosilíferos están formados en su mayoría por los restos de un gran cono de recolección, formado en el fondo del pozo. Las arcillas laminares depositadas por el agua indican que el cenote contenía agua al menos periódicamente a lo largo del curso de deposición. Dos grandes capas de fragmentos de rocas calcáreas representan secuencias de colapso del techo y los lados del cenote. Ocurrió un gran cambio en la naturaleza de los depósitos después de estos eventos, lo cual es indicado por la presencia de grandes capas superiores de arenas calcáreas ricas en microvertebrados. La evidencia tafonómica sugiere que los huesos de megavertebrados se acumularon a lo largo del tiempo debido a causas naturales. En las unidades de arcilla profunda y arcilla arenosa del sitio, los huesos de megavertebrados muestran un patrón de orientación consistente con el causado por agua en movimiento. El movimiento del agua en el cenote era de noreste a suroeste a través de grietas subterráneas en la roca caliza que formaba el cenote. La velocidad de la corriente tenía suficiente fuerza para separar los elementos menos densos, principalmente aquellos pertenecientes al Grupo I de Dispersión de Voorhies. La ausencia de huesos muy intemperizados, gastados por el agua, o mascados por carnívoros, sugiere que los huesos no permanecieron expuestos en la superficie por períodos largos antes de ser depositados en el cono de recolección, que no había una corriente fluvial fuerte, y que los carnívoros tampoco modificaron el arreglo de los huesos. La composición faunística de los taxa de megavertebrados es similar en todo el sitio, excepto en las capas más superficiales, lo que sugiere que la fauna disponible para la fosilización no cambió mucho durante el curso de deposición. Los factores tafonómicos responsables de esta muestra no cambiaron apreciablemente durante la mayor parte de la historia de deposición en Thomas Farm. Las capas superiores contienen muy poca megafauna y no son consideradas extensamente en este estudio. La evidencia faunística indica que el pozo estaba situado en una zona boscosa, y el clima durante la deposición era tropical o subtropical.

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INTRODUCTION

The Thomas Farm locality is among the best-known Miocene land vertebrate fossil sites in North America. Specimens from this deposit are housed in several major museums, and the vertebrate fauna has been described in numerous publications (see Webb 1981 for a complete list). Thomas Farm is distinctive among Florida sites for a number of reasons. The vertebrate remains are incredibly numerous and consist of both large (megafaunal) and small (microfaunal) vertebrates. Localities in which all size ranges of vertebrates are found in great abundance are very rare. Although the site has been known and worked for over half a century, fossiliferous sediments are still plentiful.

The Thomas Farm locality was discovered in the spring of 1931 by state geologist Clarence Simpson of the Florida Geological Survey, who found fragments of fossil bone on the spoil pile from a well on the abandoned farm of Raeford Thomas. These bones, and others found in a test pit dug to the west of the old well, were sent to George Gaylord Simpson, then at the American Museum of Natural History. G. Simpson identified the bones and in 1932 published the first description of the site and the fossils.

No further interest was taken in Thomas Farm until 1938, when Thomas Barbour of the Museum of Comparative Zoology, Harvard University, chanced to see the specimens in storage at the Florida Geological Survey and realized the great importance of the locality (Barbour 1944). He arranged for the purchase of the abandoned 40-acre farm, and formal excavation began. In 1942 the land was deeded to Archie Carr of the University of Florida Department of Biology, who in turn donated it to the Florida State Board of Education. In the years from 1940-1958, the site was cooperatively excavated by crews from the Florida Geological Survey, the Museum of Comparative Zoology, and the University of Florida (White 1942; Olsen 1962; Puri and Vernon 1964). It was during that time that the large collections were accumulated, both by Harvard and the Florida Geological Survey.

Excavation was conducted sporadically throughout the mid 1960s into the early 1970s under the direction of Walter Auffenberg and Thomas Patton of the Florida State Museum (now called the Florida Museum of Natural History). In 1973, field work at the site ceased and was not resumed until this study began in the fall of 1981.

Although Thomas Farm has been known for over 50 years, prior to this study only the excavations during the late 1940s and early 1950s were extensive. The large number of vertebrates removed during those years attests to the great richness of the site. In the past, the major field efforts were geared toward recovery of fauna rather than toward analysis of this isolated assemblage of sediment and fossils. The geology of the Thomas Farm locality is very complex and has never been completely understood. The mode of formation of the site and deposition of the bones has been a subject of disagreement since the locality's discovery. The still-impressive productivity of the site, the diverse fauna, and the fact that the locality is protected by the state make Thomas Farm an ideal subject for taphonomic and paleoecological analysis. This study represents the first attempt at taphonomic analysis of an early Miocene Florida terrestrial vertebrate locality. Although other early Miocene faunas are known from Florida (Simpson 1932; Frailey 1978, 1979), most of the sites have long since been destroyed by mining or land development.

The main goals of this study are to determine, by means of controlled excavation and analysis, the important geological features of the Thomas Farm locality and the mode of deposition of the megafaunal vertebrate remains. In a study of this type, a distinction is usually made between megafaunal and microfaunal analysis. This distinction is primarily methodological; most megafaunal taxa are those whose living weight was 1 kg or greater and whose bones are collected by excavation in the field, whereas most microvertebrates (weight of living animal less than 1 kg) are found by screenwashing and processing bulk matrix. Because the collecting procedures for the two size ranges of vertebrate fauna are different, the types of taphonomic data that are obtained also provide different types of information. In this study, only the results of the megafaunal taphonomy are considered. Taphonomic analysis of the rich microvertebrate fauna is discussed in detail elsewhere (Pratt 1986, 1989).

ACKNOWLEDGMENTS

S. David Webb and Gary Morgan kindly allowed use of the collections and facilities of the Florida Museum of Natural History. Members of the Thomas Farm Committee granted me permission to work at the site. Richard Hulbert, Gary Morgan, Steven Emslie, and Arthur Poyer aided in field excavations and also made many helpful suggestions. Russell McCarty provided valuable expertise in surveying and establishing the grid and prepared many of the specimens. Earlier versions of this manuscript were reviewed by Gary Morgan, Richard Hulbert, Ronald Wolff, S. David Webb, Elizabeth Wing, and Richard Kiltie. Graig Shaak provided valuable insights concerning deposition in sinkholes. Daryl Harrison drafted Figures 19 and 20 and assisted with other figures. Financial support for this project was provided by Sigma Xi, the Society of Vertebrate Paleontology Bryan Patterson award, the UF Department of Zoology, and the Florida Museum of Natural History. This paper is based on research done as part of a doctoral dissertation in the Zoology Department, University of Florida. This is University of Florida Contribution to Paleobiology Number 354.

MATERIALS AND METHODS

Abbreviations and Acronyms

The following abbreviations are used for the following museum collections that house Thomas Farm fossils: FGS, Florida Geological Survey, Tallahassee, Florida (vertebrate fossils from FGS are now housed at FLMNH); FLMNH, Florida Museum of Natural History (formerly the Florida State Museum), Gainesville, Florida; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; UF, University of Florida, Gainesville, Florida.

Other abbreviations are as follows: Directional: E, east; N, north; NE, northeast; NW, northwest; S, south; SE, southeast; SW, southwest; W, west. Quantitative; cm, centimeter; m, meter; g, gram; kg, kilogram; NISP, number of identifiable specimens, MNI, minimum numbers of individuals; P, probability; R X C, row by columns.

Field Excavations

Grid Construction

An accurate map of a fossil locality and a grid delimiting the fossiliferous sediments are prerequisites to a taphonomic analysis, as both enable the paleontologist to determine the general location of a fossil or sediment within the deposit. A topographic map constructed by the FGS in 1956 (Puri and Vernon 1964; Puri, Yon, and Oglesby 1967) eliminated the need for a completely new map. However, as no permanent measuring grid had ever been established at the Thomas Farm locality, it was necessary to do so prior to any excavation. In September of 1981, Russell McCarty and I used a surveyor's theodelite to determine the locations of the grid stakes. The stakes were placed at 5 m intervals to the north and east, respectively, of a selected 0 m North by 0 m East point in the southwestern corner of the site. The location of this point was marked by installation of a permanent concrete surveyor's post. The major axes of the grid run 25 m to the north and 20 m to the east from this 0N, 0E datum marker (Fig. 1A).

The location of each 5 m by 5 m square was identified by the coordinates, in meters north and east of the 0N,0E marker, of the northeast corner stake of each square. Each 5 m by 5 m square was subdivided into 25 1 m by 1 m squares, starting from the square designated M1 located in the southeast corner. Using this system, it was possible to record the location, to the nearest square meter, of any region of the site (Fig. 1B). For example, square meter 5 in the southwestern edge of the 15N by 10E square is designated 15N,10E M5.

The position of the grid on the FGS topographic map of the site (Puri and Vernon 1964) was determined by sighting from four relatively permanent landmarks outside the excavation area. These reference points include: (1) the eastern edge of the limestone pinnacle located on the northwestern side of the drainage ditch; (2) a cement marker near the northeast entry gate; (3) the westernmost edge of the enclosed south wall of the new pole barn; (4) a large spike driven into the large live oak tree in the southwestern corner of the site (Fig. 1A and Table 1).

Establishing a Depth Datum

To facilitate recording depth of sediment layers within the site, a depth datum point was established at 50 cm above the ground surface on the 0N,0E marker. The sediment depth at this point was arbitrarily set at 0 cm, and all other depth measurements within the site were recorded in centimeters below this 0 cm depth level. Using this point for reference, it was possible to determine the relative depth of any sediment level within the site, with the exception of the steep northern and eastern walls where no digging was planned.

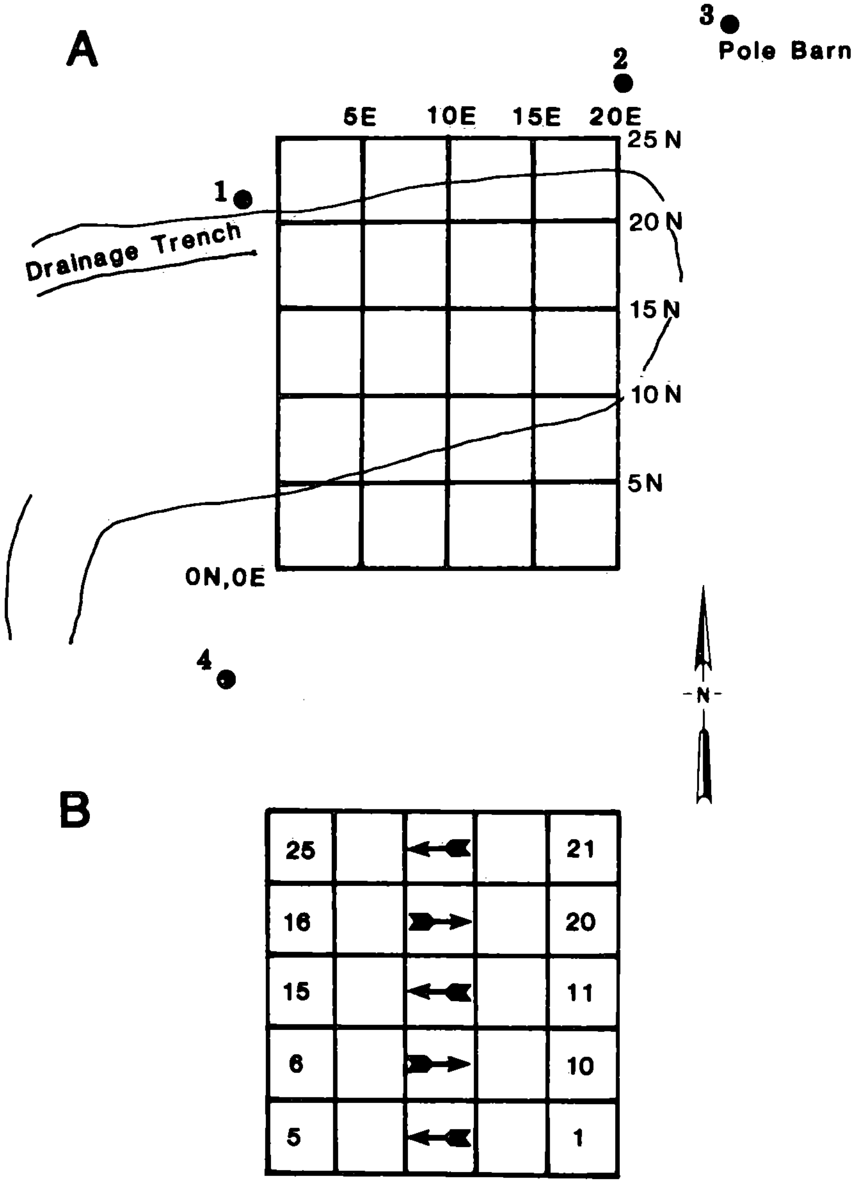

Figure 1. The measuring grid constructed at Thomas Farm in fall of 1981. (A) Outline map showing position of entire grid, composed of 5 m x 5 m grid squares. Numbered points mark locations of reference landmarks sighted from 0N x 0E datum (see Table 1). (B) Close-up of a 5 m x 5 m square showing numerical designation of square meters.

At the end of the study, elevations of excavated areas were determined. The elevation of the 0N,0E marker was established as 16.85 m (55.3 feet) above sea level. During the final stages of this study, the site was cleared and a trench was excavated (by backhoe) around the edges of the grid to aid drainage and to provide an estimate of the depth and extent of remaining fossiliferous layers (Fig. 2A). A backhoe was also used to remove large quantities of sandy matrix rich in microfauna from the northern section of the 10N x 10E square. An estimated 16 tons of this matrix were transported by truck to the grounds of UF (FLMNH Behavior Laboratory) for storage, processing and washing.

Techniques in Fossil Collecting

All workers recorded bone orientations and other relevant data in field notebooks. On any given day, a worker was assigned a square meter in which to excavate. The sedimentary unit (from 1 to 17) from which a fossil was taken was also recorded. Bones were exposed in the unconsolidated sediments with the aid of dental picks and brushes. When a fossil suitable for mapping (any identifiable fossil at least 2 cm in any dimension) was uncovered, both a field number and a reference point were marked on the bone in indelible ink using a rapidograph pen. The reference point was indicated by a small "x," and its location and orientation on the bone were described in the field notes. Bearing and plunge were also recorded. The location of the fossil's reference point was measured in centimeters north and east, respectively, from the southwestern edge of the square, and at some depth (in centimeters) below the 0 cm datum.

The bones were mapped using a system designed and constructed by Russell McCarty, Arthur Poyer, and myself. This apparatus is pictured in Figures 3 and 6, and a description is included in Appendix 1. Using this system, it was possible to record orientation data for any bone within a 10 m^2 area. Several of these measuring devices were set up in the most fossiliferous regions of the site.

All bones encountered were collected. Bones removed without complete orientation data were placed in bags labelled with the collection date, the collector's name, the 5 m by 5 m square, the square meter, and the sediment level.

Each sediment layer excavated was described and measured. The major beds are sands and clays, and the bones are concentrated in layers. The layers were named with reference to the major bone-bearing sediments. The lowest level encountered was designated as unit 1, the highest, unit 17. The total thickness of exposed sediment currently exceeds 4 m; however, the majority of the bones collected were removed from units 5 through 15, in particular units 5, 6, 7, 8, 11, and 15, through a thickness of approximately 3 m. Sediment samples for screenwashing, sediment analysis, and pollen analysis were collected from specific depths within randomly selected square meters. Strikes and dips of beds were taken throughout the course of the study, as were determinations of depths below the datum and thicknesses of particular sedimentary units. This information was used to construct a composite stratigraphic section for the site.

Laboratory Procedures

Fossil Preparation

All bones collected in the field were returned to the laboratory for cleaning, repair, identification, and cataloguing. Fossils were washed, air-dried, and identified as completely as possible. All relevant field data associated with the elements were recorded. Plaster jackets were prepared in the fossil preparation lab by technicians and by myself.

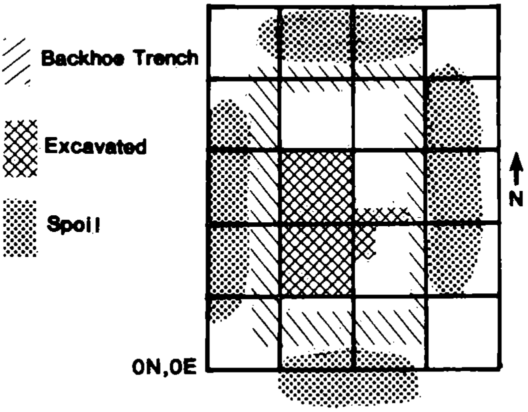

Figure 2. Areas from which fossils and sediment were removed during the course of this study. Solid black lines show the position of the grid; each square is 5 m x 5 m.

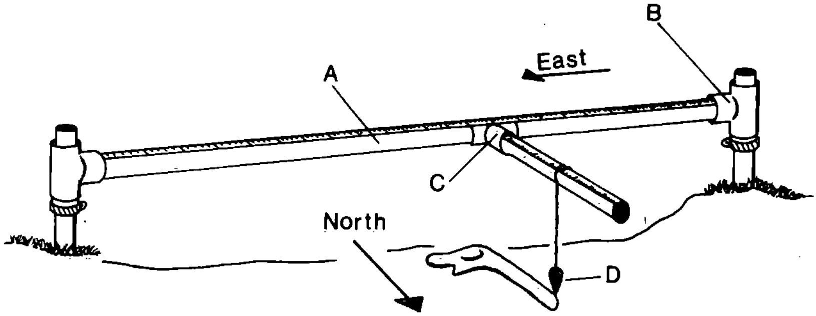

Figure 3. Permanent measuring system used to determine bone locations. (A) 5 m east-west pipe (cm ruled); (B) stationary T-joints and vertical supports; (C) moveable T-joints (PVC) and 1 m north-south measuring pipe (cm ruled); (D) plumb bob.

Table 1. Locations of references points used to mark 0N,0E datum point. Numbers correspond to those listed in Figure 1.

Reference Point	Angle (east of N) from 0N, 0E	Distance (m) from 0N, 0E	
1. Limestone pinnacle, N trench	353°	21.95	(72 ft)
2. Cement marker by N gatepost	37°	38.71	(127 ft)
3. Southwest edge of pole barn siding	39°	43.83	(144 ft)
4. Live-oak, SW edge of site	206°	7.15	(23.5 ft)

Data Processing

All information recorded for fossils greater than 2 cm in length was converted to numerical codes. Fossils were sorted into three major groups: those with field numbers and complete locality and positional data; those collected in the field with square meter and level data only; and those removed from screenwashed concentrate but belonging to taxa whose remains for the most part are large enough to be identified in the field (small carnivores and small artiodactyls). The coded data were entered and stored on an IBM mainframe computer at the Northeast Regional Data Center (NERDC). Data categories were as follows:

1. Identification data: bone identification number, family, genus, species, type of element, side (right or left), portion of element (complete, proximal, distal, and so on), greatest length of element.
2. Provenience data: sedimentary unit, 5 m by 5 m square, square meter, location within meter (in cm), depth below datum.
3. Orientation data: side of element facing up in field (medial, lateral and so on), uncorrected bearing, uncorrected plunge, corrected bearing, corrected plunge, compass orientation of reference point.

A total of over 5,000 megafaunal entries was made. Data were analyzed and sorted using Statistical Analysis System programs (SAS User's Guide 1982). Sorting procedures were used to arrange elements by data categories such as taxon, element type, or sedimentary unit. Graphics programs were used to construct histograms of preferred orientations, to plot bone positions and to calculate numbers of individuals and numbers of specimens per taxon, densities, and relative representations of bones.

Mapping

Positions of bones possessing field numbers and specific locality measurements were plotted on two-dimensional maps. Upon completion of a square meter map (all bones and sediment of a given layer removed from that square), the map was photocopied on a clear acetate sheet. The see-through map could be placed as an overlay on maps of lower sediment levels from the same square meter to show overall bone concentrations and orientations for a given excavated region. The reference points of bones were also plotted on north/south microstratigraphic sections of the site to assess relative bone concentrations within different sedimentary levels. This procedure proved to be of use in providing a check on the field identification of the sedimentary unit.

Sedimentation Experiments

In an effort to observe and document the sequence of events that occur in the deposition of a sediment cone, I constructed a small-scale replica of a sinkhole in a 10-gallon aquarium tank filled with water. The top of the tank was covered, except for an opening 5 cm in diameter through which sediment was introduced. The opening was located near one side of the tank so that only half of a cone formed, and the thickness and dip of the layers could be viewed through the glass. The initial shape of the cone was determined by introduction of a limestone "rubble layer." I subsequently dropped sand, clay, or pebble sediments through the opening periodically to form a cone approximately 30 cm in diameter.

Modern Taphonomic Studies

Although several experimental studies dealing the effects of running water on bone orientation and dispersal have been undertaken by previous workers (Voorhies 1969; Behrensmeyer 1975; Korth 1979; Pratt 1979; Hanson 1980), additional studies on skeletal element behavior in standing and moving water were conducted in order to interpret orientation patterns of the fossil bones found at Thomas Farm. I observed bone hydraulic behavior in a series of experiments using modern skeletal elements. "Fresh" deer and horse bones that retained grease, as well as elements that had been naturally weathered, were placed in water, and water uptake rates were monitored by recording weight gains to bones after varying periods of immersion. The inital tendency for an entire bone or one end of a bone to float was also noted, as was the bone's settling orientation through standing water.

Hydraulic behavior of bones in moving water was noted in two different experimental procedures. In one, conditions similar to those that occur in periodic filling and draining of a pond or sinkhole were simulated using a large (67 cm wide by 3 m long by maximum 0.5 m deep) sink. The sink had a sloping bottom (degree of slope 10°), and a drain 15 cm in diameter at the lower end. The bottom of the sink was covered with a 5 cm thick layer of fine sand. After the sink was slowly filled with water, I dropped selected skeletal elements into it. The original positions of the bones at rest were noted. Release of the plug created a strong current. Any movements of the bones in response to this current were measured and changes in bone positions noted. Each experiment was repeated three times.

I also observed fluvial effects on bone orientation and dispersal by dropping elements into a small creek on the University of Florida campus. Flow velocity ranged from 35 to 50 cm/second along the length of the stream used in these experiments. Skeletal elements of Recent deer and horses were placed in the stream in selected groups corresponding to their Voorhies dispersal groups (Voorhies 1969), and their transport was observed. Each element's position during transport and its final resting orientation were noted. Each set of bones was observed in three trials. Results of these studies were consulted in analysis of fossil skeletal abundances and bone orientations.

Faunal Composition

Numbers of identifiable specimens per species (NISP; Badgley 1986a, 1986b) of megafaunal taxa both within each major sedimentary unit and for the recently excavated portion of the site as a whole were determined. Broken fossils were examined to see if contacts with other broken elements of the same type could be made. Minimum numbers of individuals (MNI; Shotwell 1955) per species were calculated, based on the most abundant identifiable element. The similarities in faunal composition and relative abundances of megafaunal taxa between layers were assessed by the row by columns test of independence using the G-test (Sokal and Rohlf 1981:745). Faunal samples were considered significantly different from one another at the $p < 0.01$ level.

Skeletal Element Abundance

The abundances of various types of elements found in an assemblage are of use in determining the agents involved in forming a particular fossil assemblage (Voorhies 1969; Wolff 1973; Korth 1979; Maas 1985). Skeletal-part frequencies (Behrensmeyer and Boaz 1980; Badgley 1986a) of *Parahippus leonensis* elements were calculated as shown below:

$$n/\text{total }\#$$

where n = the number of each element type, and total # represents the total number of identifiable elements represented.

The relative representation of an element was calculated by determining the number of each element present relative to the number expected based on the minimum number of individuals present. The formula is:

$$100 \times n \text{ obs.}/n \text{ exp. (based on MNI)}$$

(Voorhies 1969; Wolff 1973; Korth 1979). Both abundance calculations were determined for elements of *Parahippus leonensis* within each major bone-bearing layer, and in some cases results for several similar layers were grouped to obtain larger sample sizes. Relative abundance ranks of skeletal elements obtained from fossiliferous sedimentary layers were compared statistically to ranks of abundances of elements from various modern bone assemblages using the Spearman rank-order correlation test (Sokal and Rolf 1981). Representation patterns of fossil and Recent accumulations were considered to be correlated at the $p = 0.05$ level. Abundances of element types were also compared with those characteristic of fluvial deposits (Voorhies 1969; Behrensmeyer 1975; Korth 1979; Hanson 1980).

Hydraulic Equivalents

The comparison of a bone to a quartz grain for which fluvial behavior has been determined empirically (Allen 1965) allows one to predict the range of current velocities necessary to cause transport of that bone (Behrensmeyer 1975; Korth 1979; Pratt 1979). The diameter of a grain (or sphere) of quartz that should be transported by a current also of sufficient velocity to cause transport of the bone is determined using the following formula:

$$dq_n = (P_b-1) \sqrt[3]{(1.91\ V_b/\ 1.65)}$$

where dq_n is the diameter, in centimeters, of the equivalent quartz grain, P_b is the bone density, and V_b is the bone volume (Behrensmeyer 1975). I determined the volume of *Parahippus leonensis* elements using the water displacement method. The density of a fossil bone is frequently much greater than its density prior to fossilization, so the density values used in the calculation were determined for bones of modern mammals. I calculated densities of modern *Equus* elements by weighing both dry bones and bones that had been allowed to soak in water for a day. Hypothetically, weight gains caused by water uptake may change the transport potential of a bone. The "wet" or "dry" weight of the element divided by its volume (determined by water displacement of waterlogged elements) provided both "dry" and "wet" density values. If I was not able to determine density of a particular element, I used the density calculations given by Behrensmeyer (1975:570) for zebra elements.

Bone Orientation

Orientation patterns of fossil skeletal elements were determined using a number of techniques originally used by geologists but now also employed by taphonomists (Voorhies 1969; Hill and Walker 1972; Saunders 1977; Andrews et al. 1981; Shipman 1981; Shipman et al. 1981). The presence of preferred bone orientation is inferred by construction of a mirror-image rose diagram. The rose diagram records bone compass orientations in 10-degree increments from 0 to 359 degrees east of North (Shipman 1981). Rose diagrams were constructed for all bones with orientation data, long bones with orientation data, bones from specific sedimentary layers, and for various types of elements. Orientation patterns of bones were compared to the pattern of elements expected in a uniform, or non-preferred orientation pattern (random orientation pattern of Shipman 1981) using the Chi-square goodness of fit test (Sokal and Rohlf 1981:710). Orientation patterns were considered significantly different from uniform at the $p <= 0.01$ level. Frequency of orientation to a preferred end was also assessed by determining percentages of orientations of ends of bones to each of the four compass quadrants (NE, SE, SW, NW). Bone bearings and plunges were also plotted on stereonets using the technique for plotting bearings and plunges of lines (Voorhies 1969; Ragan 1973:95).

RESULTS AND DISCUSSION

Previous Excavations and Interpretations

Although the Thomas Farm locality was discovered over fifty years ago and has been worked intermittently since that time, procedural information concerning the excavations is limited. This historical account of the site has been obtained from various publications, notes, photographs, and anecdotal references.

Field work at Thomas Farm was initiated in 1931 by geologists Clarence Simpson and G. M. Ponton. An account of the results of their work, later published in George Simpson's discussion (1932) of the Thomas Farm mammalian fauna, included a description of a 6-foot stratigraphic section showing 9 sedimentary layers. The section was obtained from a trench that was evidently dug on the western edge of the site, as a major feature of the eastern portion of the site, the boulder layer, is not mentioned in the description.

G. Simpson (1932) offered two hypotheses concerning the mode of deposition of the locality. In the first, he suggested that the fossils had accumulated as a result of the breakdown of the marine Hawthorn Formation and subsequent reconcentration of the bony elements in the underlying Ocala Limestone. This idea was later discarded, as no Miocene age marine fossils are known from the locality. The alternate interpretation, one that would be repeated and elaborated upon in subsequent publications, was dubbed "the sinkhole hypothesis." Simpson noted that the fossiliferous sediments were located in a large, roughly circular area about 250 feet (80 m) in diameter and roughly 15 feet (5 m) lower in elevation than the surrounding ground surface (G. Simpson 1932). He suggested that the depression marked the site of an ancient sinkhole. According to G. Simpson, this interpretation was supported by the fact that the vertebrate fossils were concentrated in specific layers, and characteristics indicative of fluvial transport and deposition were lacking.

Following a 6-year hiatus, excavation at the site was renewed in the late 1930s by field parties from the Museum of Comparative Zoology at Harvard University. White (1942:Plate 14) published a map and a stratigraphic section of the site based on analysis of auger samples taken by C. Simpson. The exact placement of the early excavation cannot be identified with certainty, as neither White's map, nor the original map from which the published version was constructed, contain any landmarks. Based on the stratigraphic section and photographs of the locality taken in the 1940s (Barbour 1944:11), it seems likely that much of the excavated region was in the vicinity of the boulder layer.

The stratigraphic section published by White (1942) does not contain fine-scale sedimentological details compared with what is known about the sedimentary layers at present, but it does provide important documentation of the early excavations undertaken by MCZ workers. Several of the sedimentary layers pictured in White's section were not encountered in subsequent excavations. The sedimentary unit referred to by White as the clayball layer, located on the easterly surface of the boulder bar, was evidently not extensive and was removed in early excavations. White also discussed the presence of a cap of phosphatic sandstone at the southeastern edge of the site. He identified this layer as the marine Hawthorn Formation (Hawthorn Group of Scott 1988), an assignment rejected by later workers (Bader 1956). Although no sediments assignable to the Hawthorn Group are found within the locality today, a recent core taken by the FGS in February 1988 approximately 100 m to the south of the site (Thomas Farm #3) encountered a massive unit of phosphatic marine sediments. Preliminary investigation indicates that these sediments are not part of the Hawthorn Group, but their extent and their relationship to Thomas Farm sediments is not clear (T. Scott pers. comm.).

White (1942) did not subscribe to C. Simpson and Ponton's earlier hypothesis (G. Simpson 1932) that the site was formed as a result of sediment deposition in a sinkhole, suggesting instead that the sediments represented a sequence of several cycles of cutting and filling by a fluvial system. He cited the presence of lenticular clays, the lack of sorting of the sediments, and the presence of the boulder layer as support for this interpretation. White proposed that a stream initially carved a channel in the Ocala limestone, and eventually silted up, depositing sands and bones as the current slowed. According to his interpretation, the stream was later rejuvenated, and current velocities increased sufficiently to cause transport and eventual deposition of a bed, approximately 2 m in thickness, composed primarily of cobble-sized limestone boulders (White 1942:Plate 14). White also stated that subsequent loss of stream competence resulted in deposition of the lower energy clayball and sand layers that were later truncated by intrusion of marine Hawthorn Formation sediments.

A. S. Romer (1948) of the MCZ summarized all previously published interpretations concerning the mode of deposition of the Thomas Farm locality and expressed support for the fluvial hypothesis. He also reported an areal extent for the site that approached an acre, and a depth of unexcavated fossiliferous sediments exceeding 40 feet. This information was evidently obtained by analysis of cores, presumably those taken by C. Simpson in 1941, although Romer did not identify the source of his information. It appears that he overestimated the area, but not the depth of the site. A recent FGS core sample (Thomas Farm #2) taken in February 1988 from the southwestern portion of the site contained over 10 m (33 ft) of fossiliferous sediments.

In 1956, Robert Bader of the UF Department of Zoology, who participated in the Thomas Farm excavation for several years and published an analysis of the equids, reviewed the hypotheses concerning formation of the locality (Bader 1956). Bader favored the sinkhole interpretation, but also suggested that the sinkhole had been stream-fed. He rejected White's identification of the uppermost layer as the Hawthorn Formation, contending that the area had not been covered by the mid-Miocene sea.

The years 1955 through 1957 were very active field seasons for the MCZ and the FGS. During that period, a permanent topographic map of the site was constructed based on a USGS benchmark located on State Highway 129, some two miles away. A number of auger samples were taken in 1956 and analyzed by FGS geologists (Puri and Vernon 1964; Puri et al. 1967). Photographs taken by Bryan Patterson of the MCZ show the locations of major excavation trenches (Fig. 4). Several of these trenches have been relocated in recent work at the site.

Stanley Olsen, a fossil preparator at the MCZ, joined the FGS in 1956. He expanded Bader's (1956) view of site formation into a more elaborate interpretation of the mode of deposition of the Thomas Farm, describing the site as a combination sinkhole-stream-cave complex (Olsen 1959, 1962). This interpretation placed more emphasis on the vertebrate fauna known to occur at the locality than on sedimentological evidence. Walter Auffenberg of the FLMNH (1963a, 1963b), who agreed with Olsen's views, published an educational booklet containing an illustrated reconstruction of the site in which he diagrammed the events involved in sinkhole formation. Richard Estes (1963) described the salamander and lizard component of the herpetofauna and suggested, without first-hand knowledge of the site, that deposition had taken place in a spring-fed, seasonally water-filled sinkhole.

Two FGS publications released in the 1960s (Puri and Vernon 1964; Puri et al. 1967) contained maps and stratigraphic descriptions of the Thomas Farm locality, prepared principally by S. J. Olsen. Puri and Vernon (1964) interpreted several sedimentological features of the site as indicative of fluvial deposition. They described three major, supposedly fluvial, sedimentary facies at the locality: a water-lain blue-green clay, a point bar composed primarily of limestone boulders (the "boulder bar"), and calcareous sand layers that they described as "crossbedded." In addition, based on the presence of bat fossils at the locality, they suggested that the stream was directly associated with a cavern.

From the late 1950s through the 1960s, fieldwork at Thomas Farm was conducted very sporadically. The site was cleared in preparation for the 1964 Society of Vertebrate Paleontology field trip. The Field Trip Guidebook published for the meeting (Auffenberg et al. 1964) discussed the major sedimentary and faunal characteristics of Thomas Farm and reviewed the hypotheses of site formation. Thomas Patton of the FLMNH, who provided

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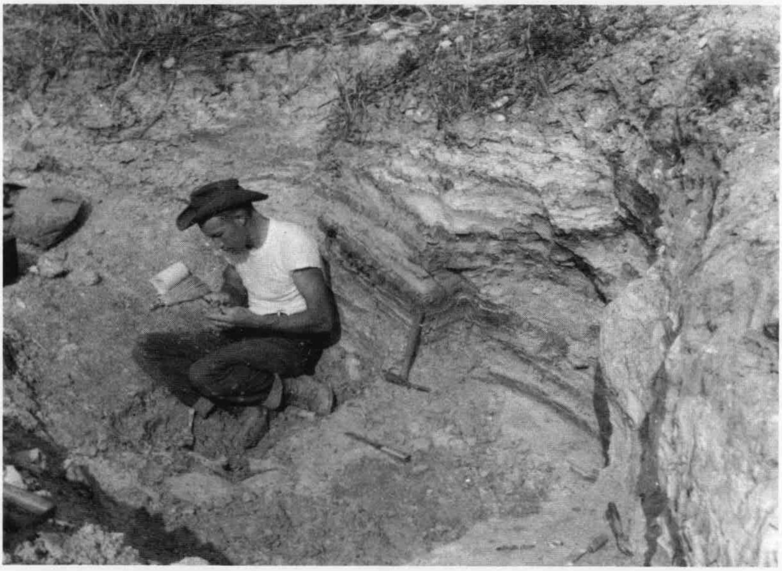

Figure 4. Photographs of the Thomas Farm excavation taken during the 1956 field season. (A) View to southwest showing drainage ditch. (B) Trench in northeastern region of the site. Note dipping beds by rock hammer. Photographs by Bryan Patterson, courtesy of Museum of Comparative Zoology, Harvard University.

much of the material for the Guidebook, made a small collection from the site in the middle 1960s.

In the summers of 1971 through 1973, Auffenberg and FLMNH crews spent several weeks in the field at the Thomas Farm locality. Notes taken by Auffenberg and David Frailey during the 1973 field season show the location of their dig for that year. Auffenberg and Frailey used the limestone outcrop in the northern edge of the site as a reference point for the northwestern stake of a grid system, and a point 30 feet due south of the original northern gatepost as the northeastern stake. The grid was composed of 10-foot by 10-foot squares designated by the letters A through F from west to east, and by the numbers 1-5 from north to south. It is unclear whether the grid possessed 6 or 7 west-east squares. The map of the grid in the field notes lists only 6 (A through F); however, the distance between the northwestern and northeastern corners of the grid exceeds 70 feet, indicating either an error of well over 10 feet was made in measuring, or that the grid system actually contained seven east-west squares. Upon completion of their dig, they covered the excavated area with a sheet of bright blue plastic.

Although the grid measurements obtained from the field notes are not exact, the approximate location of the 1973 grid and excavation is shown on a

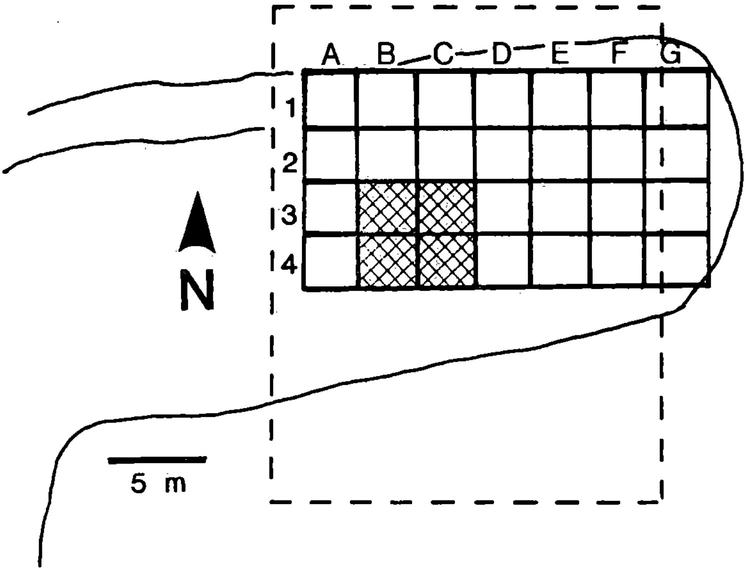

Figure 5. Location of Auffenberg field party 1973 grid (solid lines) superimposed on grid outline used in this study (dashed lines). Cross-hatched area indicates region excavated in 1973 summer field season.

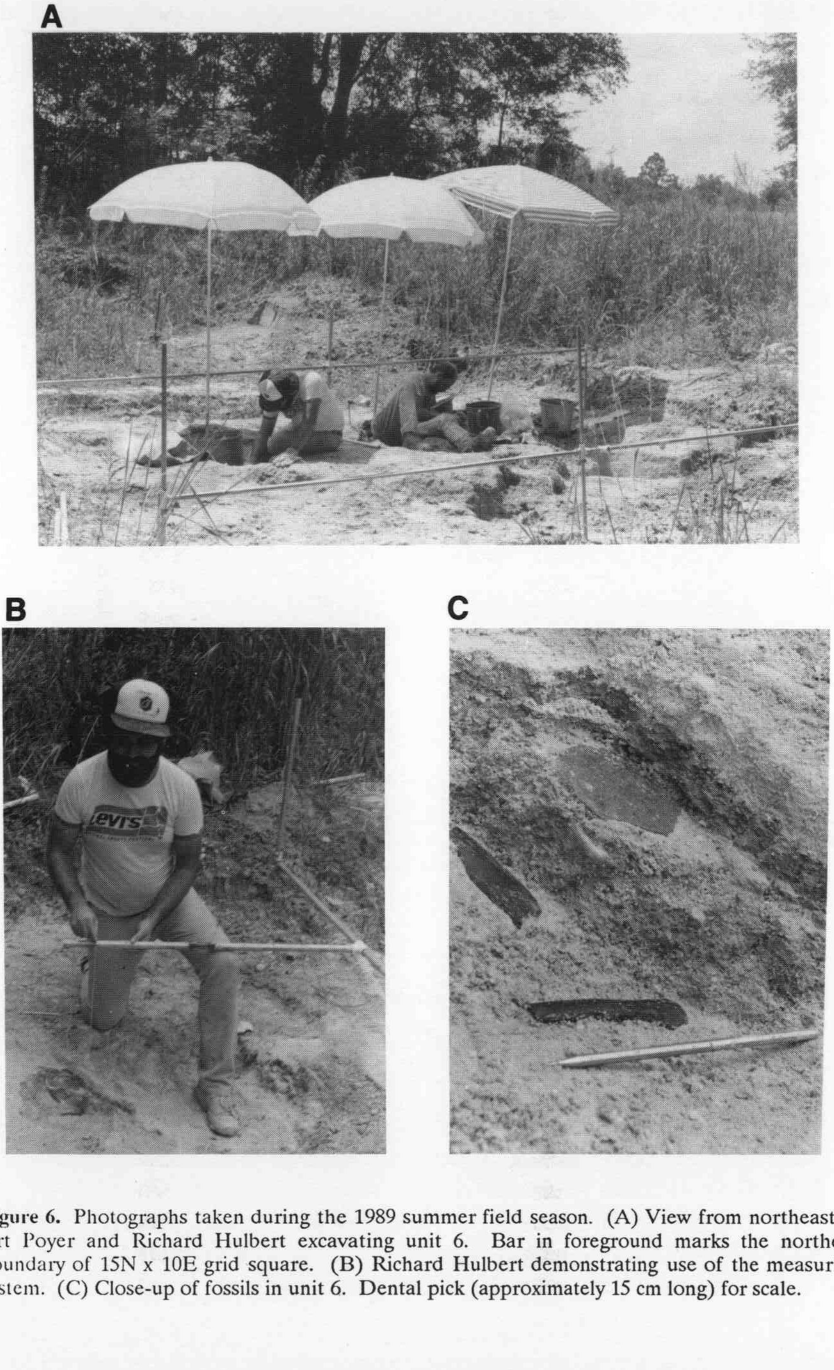

Figure 6. Photographs taken during the 1989 summer field season. (A) View from northeast of Art Poyer and Richard Hulbert excavating unit 6. Bar in foreground marks the northern boundary of 15N x 10E grid square. (B) Richard Hulbert demonstrating use of the measuring system. (C) Close-up of fossils in unit 6. Dental pick (approximately 15 cm long) for scale.

map of the site (Fig. 5). Several of Auffenberg's trenches, indicated by remnants of blue plastic, have been relocated in the most recent excavation, although none of the marking stakes were recovered in place. Sediment levels in Auffenberg's dig were designated by i, ii, and iii from highest to lowest levels. The criteria used to identify these levels are not stated in the field notes, and I was not able to correlate the three levels with my described units.

From the middle 1970s to early 1980, no excavations were undertaken at Thomas Farm. In 1980, Thomas Farm was extensively cleared in preparation for a field trip conducted during the 40th annual meeting of the Society of Vertebrate Paleontology (Webb and MacFadden 1980). Excavation for the current study began in 1981 and continued on a regular basis through 1985. Photographs in Figure 6 show the site as it looked in 1989.

In the course of the most recent excavation, I employed the digging and collecting techniques described above in the Materials and Methods section. Information obtained on the sediments excavated was used to construct a detailed stratigraphic section for the site, shown in Figure 7. Recent field work has brought to light a number of features which must be taken into consideration in the interpretation of the environment of deposition. Several of these features are related to the geology of the locality, while others pertain to the taphonomic agents involved in forming and modifying the Thomas Farm bone assemblage.

Environment of Deposition

The Thomas Farm sediments are very localized and most cannot be traced laterally over distances greater than 20 m. The geology of the Thomas Farm locality is complex and study of the sediments is hindered by the fact that large portions of sedimentary layers were removed in previous excavations. The composite stratigraphic section of the site (Fig. 7) shows a number of features that warrant detailed consideration in a geological analysis:

1. Extensive boulder layers of the upper unit of the Eocene Crystal River Formation and the Oligocene Suwannee Limestone are found in the central portion of the site (units 8 and 11). In-place limestone outcrops are located to the north and west of the deposit.
2. Sedimentary layers dip to the south-southwest.
3. The sediments in the lower portion of the section consist of alternating sequences of clay and sand layers (units 1 through 8a). These layers are rich in large vertebrates, but microvertebrates are comparatively uncommon.

4. The upper boulder layer is overlain by massive beds of calcareous sand containing abundant microvertebrates (units 12 through 15). Large vertebrate remains are rare in these layers.

1. In-Place Limestone and Limestone Boulder Layers

The limestones at the Thomas Farm locality, both the in-place Paleogene limestone and that redeposited in the Miocene boulder layers, provide information concerning the mode of deposition. Although limestones of three different ages are present within the site, only the oldest is still found in place anywhere in the region (Puri and Vernon 1964; Puri et al. 1967). The exposed outcrop of limestone located on the northwestern side of the northern drainage ditch extends approximately 3 m above the present ground surface, and contains the invertebrate fossils *Oligopygus wetherbyi* (an echinoid) and *Amusium ocalanum* (a pectinid bivalve), index fossils of the middle unit of the late Eocene Crystal River Formation (Puri and Vernon 1964; Williams et al. 1977). A core sample taken to the west of the excavated area (Thomas Farm #1) in February 1988 hit limestone at 2.5 m below the surface. The limestone in the core cannot be identified, but because it exceeds 5 m in thickness, it is most likely in-place middle Crystal River limestone. White (1942) also reported encountering limestone at about 7 ft below the ground surface in the western portion of the excavation.

Unit 8, the lower massive boulder layer within the site itself (Figs. 7, 8) is composed primarily of the upper unit of the Crystal River Formation of latest Eocene age, as evidenced by presence of the annelid worm *Rotularia vernoni* (Nicol and Jones 1982). This layer is thickest in the easternmost region of the excavation (over 1 m in thickness), but pinches out toward the west. The boulders vary from completely unweathered angular fragments to weathered subangular boulders. The surrounding matrix is a fine limestone sand, although thin clay drapes are found in some regions of the boulder layer. Excavation of this level has not been extensive, and it is not clear at this point if mean boulder size changes within the layer. It appears that many of the boulders have also undergone post-depositional breakdown as the result of ground water solution. The vertebrate fossils found in the boulder layer have been crushed and flattened by post-depositional compaction.

In addition to the rubble layer, two large fragments of upper Crystal River limestone have been found near the southern boundary of the excavation. One was encountered in the course of excavation of a north-south trench through the eastern section of the 10N,10E and 5N,10E squares. This fragment measures nearly 2 m across, but its thickness has not yet been determined.

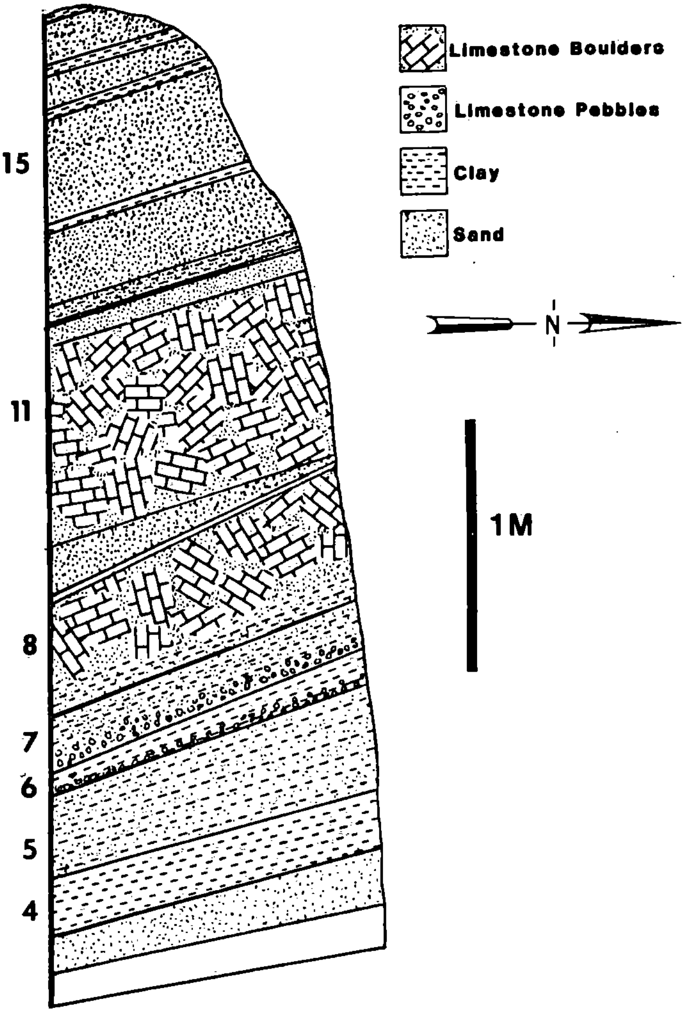

Figure 7. Composite stratigraphic section of sediments excavated in this study. Scale = 1 m.

Another huge fragment of upper Crystal River limestone was removed by a backhoe in the excavation of the southeastern portion of the eastern drainage trench. This "boulder" exceeds 3 meters in diameter and may have been broken off the piece of limestone exposed in 5N,10W. Neither of the 2 huge fragments were *in situ*, as they both were recovered from regions of the site that are considerably lower than the top of the older in-place middle Crystal River outcrop.

The upper boulder layer, unit 11, is composed almost entirely of the friable Oligocene Suwannee Limestone, characterized by the irregular echinoid

Figure 8. Vertical section showing lower boulder layer (unit 8), sand and clay layers (units 9 and 10), and upper boulder layer (unit 11). North to right side of page, scale (white line) = 10 cm.

Rhyncholampus gouldii (Puri and Vernon 1964). This boulder layer is similar to the underlying unit 8 rubble layer, except that many more of the boulders are rounded and show evidence of extensive solution. A number of the boulders are quite large in size (over 25 cm in diameter). The thickness of this boulder layer thins to the west where it is replaced by a layer of fine white limestone sand. Large numbers of vertebrate fossils are found in unit 11, although they are generally badly crushed.

Neither the upper unit of the Crystal River Formation, the *Rotularia vernoni* Zone of Williams et al. (1977), nor the Suwannee Limestone occur in-place today at Thomas Farm or in the surrounding region. Based on the presence of Suwannee Limestone in the boulder layer and its absence from nearby in-place outcrops, White (1942), and later Puri et al. (1967), stated that the boulders had been carried to the locality from some distance away by a fluvial system of extremely high competence. These workers apparently were unaware that actually two boulder layers are present, and that the lower is composed of upper Crystal River-age limestone. The thickness of the boulder layers, coupled with the large size of the boulders and limestone fragments, indicate that fluvial transport is unlikely to have been responsible for deposition of these sedimentary layers. Rather, during the early Miocene a complete stratigraphic section of middle Crystal River Formation through Suwannee Limestone existed at the site. The only remnants of the upper Crystal River Formation and the Suwannee Limestone are those that fell into the deposit and were preserved. The remaining in-place sections of these two limestone units were removed by erosion. The nearest measured section containing a reasonably complete sequence of these units occurs in a quarry near Mayo, in Lafayette County, about 75 km northwest of Thomas Farm. Using the thickness of the Mayo section and the type section of the Crystal River Formation (Puri and Vernon 1964) in Citrus County, Florida, as general guides, the in-place limestone sequence at Thomas Farm in the early Miocene may have been as much as 30 m thick.

Numerous previous workers (Simpson 1932; White 1942; Bader 1956; Olsen 1959; Puri and Vernon 1964) have noted the presence of limestone at Thomas Farm and have attempted to relate it to the mode of deposition. In fact, the entire north-central region of Florida is underlain by limestone that has been subject to solution since the late Oligocene (Cooke 1945; Puri et al. 1967; Lane 1986), and sinkholes and caves are common features of the north Florida karst terrain (Davis 1930; Puri and Vernon 1964; Puri et al. 1967, Williams et al. 1977; Sinclair et al. 1985; Beck and Sinclair 1986; Lane 1986). It is likely that Thomas Farm is indeed the site of an ancient sinkhole, perhaps of the collapse doline variety. A sinkhole that forms through limestone collapse generally possesses high, steep sides and may act as a trap, while a sinkhole that forms through solution of limestone and the weight of overlying non-limestone sediments tends to be funnel-shaped, and may form a shallow pond near the ground surface (Stringfield et al. 1974; Bogli 1980; Sinclair et al. 1985; Trudgill 1985; Beck and Sinclair 1986; Lane 1986). The boulder layers obviously represent collapse events, but probably do not mark the initial collapse phase that caused formation of the sinkhole, as these layers lie above the fossiliferous sand and clay sediments. Recovery of a deeper, extensive boulder layer at the base of the fossiliferous sediments would substantiate the interpretation of Thomas Farm as a collapse sink. If the unit 8 and 11 boulder layers are remnants of a collapsed cave roof, then it must be assumed that the sediments below unit 8 were deposited in a closed cave system. However, the absence of speleothems, as well as several other features discussed later, suggest that such was not the case.

2. Dip of Beds

One of the most obvious features of the Thomas Farm sediments is that all beds excavated exhibit a pronounced dip to the south-southwest (Fig. 9A). Steepness of dips of the various beds range from 12 to 22 degrees, averaging about 15 degrees. The beds strike from 255 degrees east of North to 310 degrees east of North, with the majority striking 270 degrees, almost due west (Table 2). The dip of the beds may be clearly seen in White's stratigraphic reconstruction of the deposit (White 1942:Plate 14), and in photographs taken during the 1956 field season (Fig. 4); however, among previous papers on the Thomas Farm, only the 1964 SVP Guidebook (Auffenberg et al. 1964) makes reference to this characteristic. Other workers (Puri and Vernon 1964; Puri et al. 1967) incorrectly interpreted the dipping beds as crossbedding.

The Thomas Farm sediments exhibit two major directons of dip. The lower layers dip southwest at about 220 degrees east of North. A change in dip direction occurs in the upper part of the massive sand layer designated as unit 5. Upper unit 5 and higher layers dip on average 180 degrees east of North. Since there is no evidence of substantial regional dips in north-central Florida, the presence of steeply dipping beds requires explanation.

One hypothesis, involving tilting by post-depositional tectonic activity, is quite unlikely for a number of reasons. Such phenomena are rare in Florida's geological history. Evidence for subsidence would be provided by large-scale faulting over an extensive area. There are small faults in several regions of the site, but they appear to be associated with local post-depositional compaction and are hardly part of a regional pattern. The fact that there are two different sets of bed orientations within the site also indicates that these are local intraformational structural features.

An alternative explanation is that the dip of the beds reflects their original position at the time of deposition. Acceptance of this hypothesis limits the

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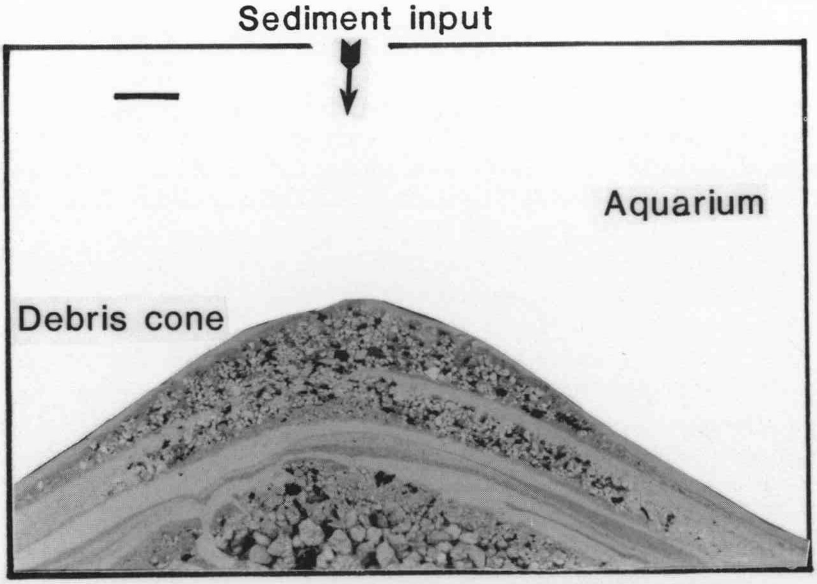

Figure 9. (A) Vertical section showing dipping beds at Thomas Farm. North to left of page, scale (black line) = 10 cm. (B) Debris/sediment cone model formed under laboratory conditions. Note dipping sedimentary layers. Scale = 5 cm.

number of geologic conditions under which the fossiliferous sediments may have formed. Fluvial deposits do not commonly possess sets of beds that uniformly dip steeply over distances of several meters, and beds laid down in standing water are ordinarily level except for slumping. The two most common non-marine geologic conditions under which beds show consistent dip are deltas and alluvial fans (Twenhofel 1932). There is no evidence to suggest that either of these two features are represented at Thomas Farm. Both require large streams or rivers, and the latter is characteristic of arid mountainous regions. A third means by which large sets of beds may be deposited on an angle is seen in regions of karst and involves formation of a debris cone at the bottom of a sinkhole (Sweeting 1973; Brain 1981). If the opening to a sinkhole is relatively constricted, sediment influx is confined to a limited area and sediment accumulates primarily in a cone-shaped pile on the floor of the sink. A small-scale debris cone model formed in an aquarium (see Materials and Methods) shows that sedimentation under the above described conditions does result in a cone-shaped structure composed of uniformly dipping sediment layers (Fig. 9B).

Debris cone deposition is generally initiated in a collapse sinkhole when the limestone roof of a closed chamber (cave) within the limestone collapses. This cave-in results in a pile of boulders that forms the base of the cone, and also provides an opening through which sediment from the surface may be introduced.

Table 2. Strikes and dips taken on major sedimentary units. s.d. = standard deviation of mean.

Sediment Unit	No. of Observations	Mean Strike degrees E of N	s.d.	Mean Dip	s.d.
1	1	314		24 SW	
2	2	314		9 SW	2.0
3	3	311	19.6	13 SW	2.6
4	2	309		13 SW	0.5
5 (lower)	5	312	4.8	16 SW	1.2
5 (upper)	8	280	6.9	15 SW	3.1
6	1	272		22 SW	
7	12	265	9.7	21 SE	5.2
8	10	279	13.6	18 SW	4.9
9	3	261	7.3	20 SE	1.7
10	7	266	7.2	23 SE	4.8
11	4	289	32.1	14 SW	2.8
12	7	282	7.9	19 SW	3.4
14	8	281	5.2	23 SW	4.0
15	3	273	12.6	22 SW	3.7

Under ideal conditions, a debris cone that forms in the center of a sink is conical and exhibits a number of recognizable features. In a natural environment, perfect symmetry is neither expected nor seen, but a number of characteristics pertaining to the dip of the beds and general shape of the cone can be identified.

As one moves across the surface of a cone at any given depth, the compass direction of dip should change. This relationship is illustrated in Figure 10A. Dip direction also changes more rapidly near the apex of the cone (distance 1 in Fig. 10A) than near the base of the cone (distance 2 in Fig. 10A). Applying this model to the Thomas Farm locality, it is expected that directions of maximum dips recorded in the eastern regions of the site would be more easterly than those taken in more western sections of the site. Due to the relatively small area excavated, the maximum distance across which a given bed can be measured seldom exceeds 5 m. Those layers in which several strikes and dip measurements were taken at east-to-west distances of 5 m or greater are units 7 and 8. These beds show an easterly to westerly trend in dip directions, although there is also some minor local variation. The total difference in dip direction in unit 7 across an east-to west line 8.3 m long is 31 degrees, and in unit 8, the dip direction changed by 14 degrees over a 5 m east-west distance. Based on the amount of change in east-to-west dip directions of the various layers, the circumference of the cone taken at the level units 7 and 8 in 15N,10E M11-15 may be estimated using the following formula:

$$\text{Circumference} = \frac{\underline{a\ (\text{pi})}}{\sin\ (b/2)}$$

where a is the maximum east-west distance between two dip readings, and b is the change in dip direction across a. The circumference estimates of the cone in units 5, 7, and 8 range from 97.5 to 128 m. Therefore, if a complete cone formed in the middle of the sink, the bottom of the sinkhole may have been as wide as 30 to 40 m, well within the size range of collapse sinkholes found today in north Florida (Lane 1986).

Figure 10B illustrates another characteristic of dipping beds on a debris cone. In heading north along a level line that passes through the central longitudinal axis of a cone from a given point on the surface of the due south face, dip direction should suddenly change to the north if the cone is symmetrical. Assuming the above estimated calculations of debris cone size are reasonably accurate, the length of line xy measured from point x on the south face of the cone in unit 7 to point a point (y) on the same level of the north face in unit 7 is 30 m. It is unlikely that north-dipping sediments, if any exist, will ever be exposed. A pole barn and a driveway are located 17 m to the north of the excavation, and the present elevation of this region is over 5 m higher than that of the dig.

It is possible that the debris cone did not form in the center of the sink, but that factors governing sediment deposition caused buildup of a partial cone

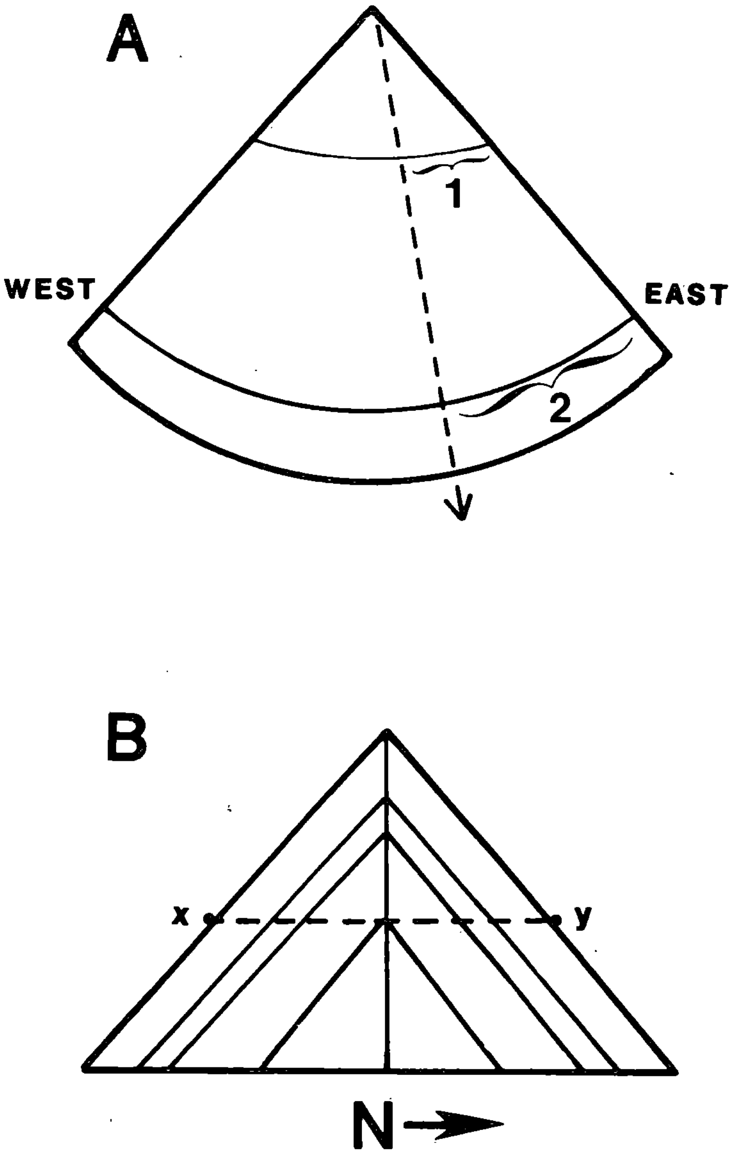

Figure 10. Changes in dip directions of beds deposited on a sediment cone. (A) Diagrammatic representation of degree of change in dip direction across various levels on the surface of a sediment cone. (B) Diagram illustrating the 180° change in dip direction on either side of the cone's central axis.

or talus slope against the northern wall of the sinkhole, and thus the northern-dipping beds were truncated. The map of the locality (Fig. 1, point 1) shows the location of the pinnacle of middle Crystal River limestone on the northern edge of the pit. This outcrop is probably a remnant of the northern wall of the sink. An FGS auger sample taken approximately 15 m to the north of the site in 1956 (Puri and Vernon 1964; AS-297) reportedly hit limestone at an elevation of 11.9 m (39 feet) above sea level (7.6 m below ground surface). However, as the type of limestone was not identified, it cannot definitely be stated whether it was in place or part of a rubble layer.

As noted previously, there is a change in dip attitude of all beds above unit 5a (Table 2). Dip directions of the lower layers average 220 degrees to the southwest. Starting with the upper layers of massive unit 5, the dips change to a more southerly (175-190 degrees east of North) orientation, and average this reading throughout the remainder of the stratigraphic sequence. The change in dip direction may be the result of a change in the location of initial sediment input, as shown in Figure 11, which schematically illustrates results of laboratory experiments with the sinkhole model. Either an increase in the size of the opening through which sediment falls, or displacement of the position of the opening toward the west results in the formation of a second cone that partially overlies the first. Dip directions of beds forming the upper cone are shifted eastward relative to dips of beds in the lower cone. It is not unlikely that the source of sediment input at Thomas Farm may have shifted slightly to the west, either by the formation of a larger opening at the top of the sink, or by blockage of the previous opening, causing a change in the direction of dip of the beds. Presumably, enlargement of the opening would involve introduction of limestone rubble into the site; however, there is no evidence that a rubble fall occurred at the time the bed dip shifted. Sediments of units 5a and 5b are very similar in lithology and neither contain large boulders of limestone. The original opening may have been constricted by slippage of a large fragment of limestone that initially blocked the eastern portion of the sink entry. This huge boulder may have subsequently fallen and formed the lower boulder layer in unit 8.

Evidence that the Thomas Farm sediments form a debris cone is also provided by features of the two boulder layers. In the eastern region of the site where boulders are thickest (Fig. 12A) the sand layer is extremely thin, but it thickens gradually toward the west, attaining a maximum thickness of about 25 cm. Both boulder layers thin toward the west. This type of relationship was reproduced in the laboratory with the sinkhole model (Fig. 12B). Boulders pile up just below the point of input but pinch out along the lower surface of the cone. Sandy sediments that fall on top of the boulder layer are thickest along the the lower surfaces and near the base of the cone. The introduction of a second boulder layer on top of the sand causes compaction of the sand at the point of initial input, and some of the sand makes its way into the interstitial

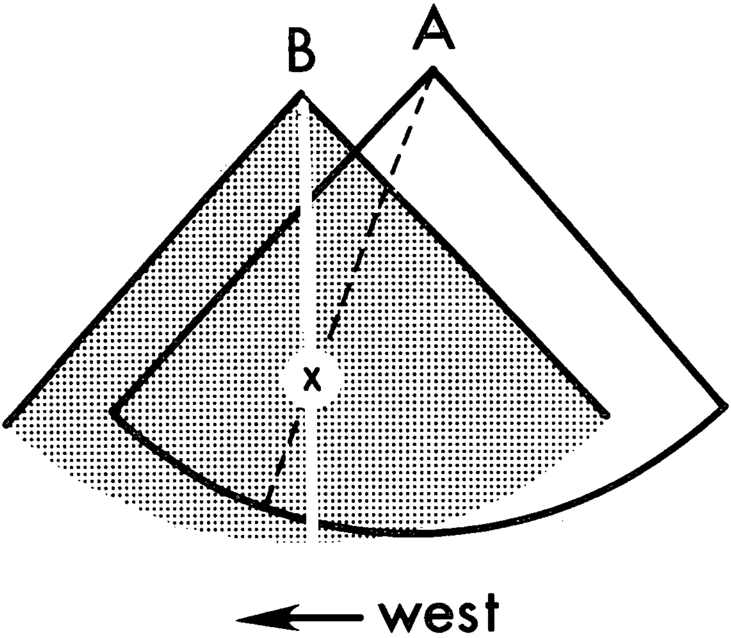

Figure 11. Possible mechanism by which dip of beds may change at one point or location on the sediment cone. Sediment input at point A results in formation of sediment layers whose dip at point X is 220° E of N (dashed line). A westerly shift in sediment input (point B) results in deposition of sediments with more easterly dip directions at point X (white line).

spaces between the lower boulders. However, the sand layer remains thick on either side of the apex. This difference in the relative thickness of sand and boulder layers is also due in part to the differing angles of repose achieved by the two sediment types. The relationship of the sand and boulder layers corroborates other evidence of a complex debris cone within the site.

3. Clay Layers

The sediments found below the boulder layers are predominantly clay and sandy-clay layers (Fig. 13). Many of these beds are composed of numerous

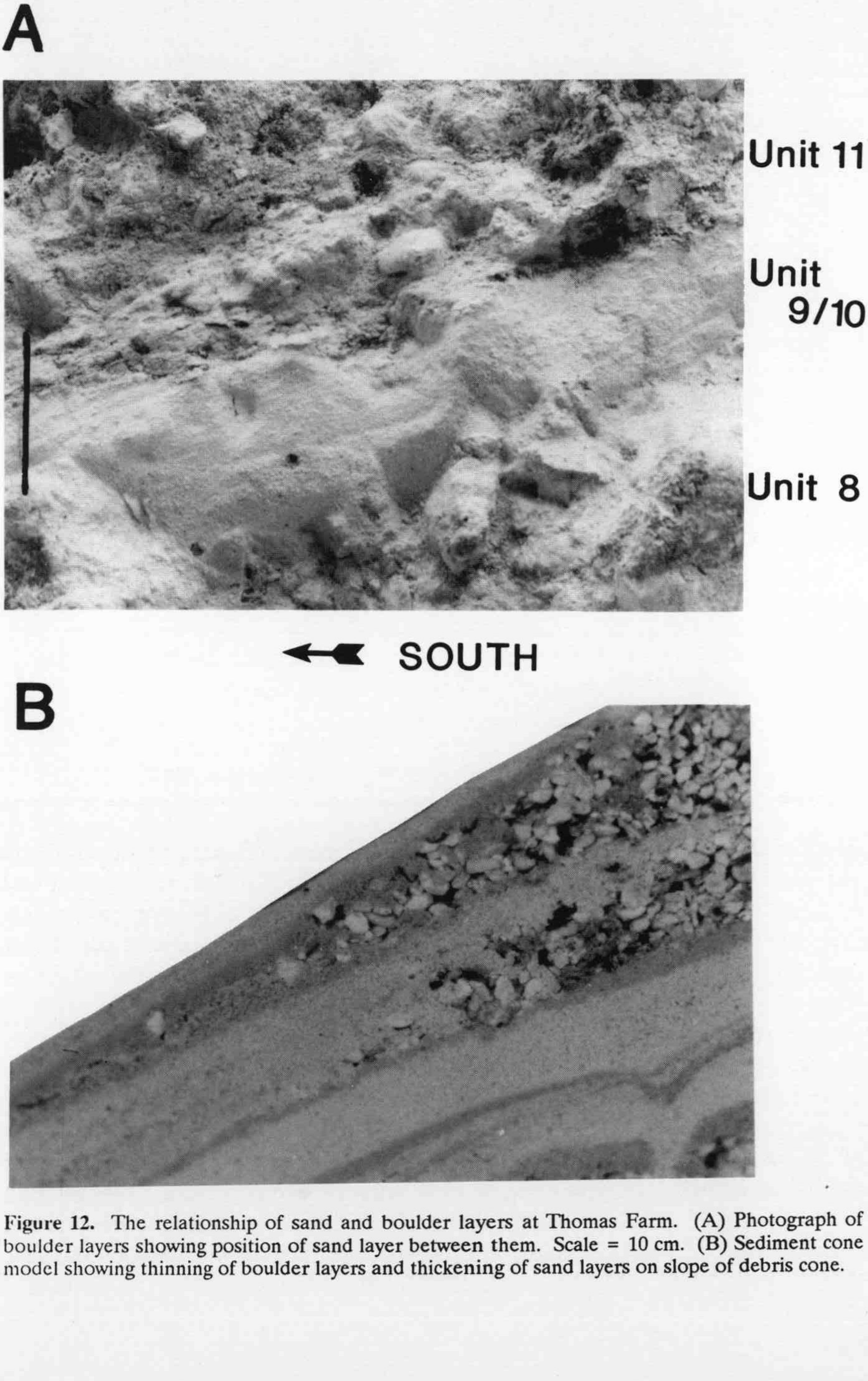

Figure 12. The relationship of sand and boulder layers at Thomas Farm. (A) Photograph of boulder layers showing position of sand layer between them. Scale = 10 cm. (B) Sediment cone model showing thinning of boulder layers and thickening of sand layers on slope of debris cone.

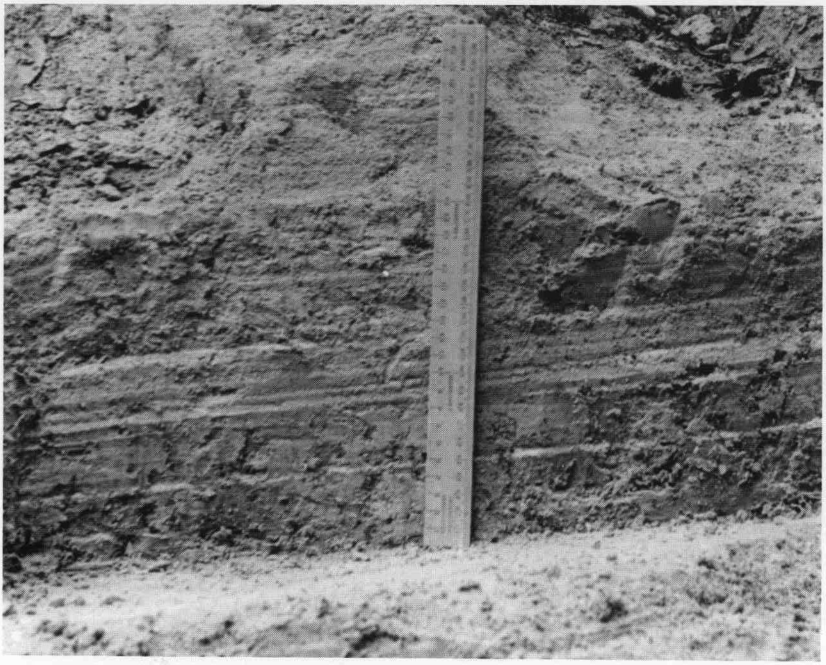

Figure 13. Vertical section showing laminated sand and clay layers at Thomas Farm. Shown is unit 5, scale = 30 cm.

fine laminae, characteristic of water-lain sediments (Dunbar and Rodgers 1957). Vertebrate fossils of medium- to large-size animals are found concentrated in specific layers. Units 1 through 4 have been exposed only recently, and were not extensively excavated in this study. Units 5a and 5b are both laminated orange sandy-clays. The two portions of unit 5 were given separate letter designations because of the change in dip direction that occurs between them. Total thickness of unit 5 averages about 43 cm. It is more sandy than some of the upper layers, and closer inspection reveals that this unit is composed primarily of thin (1-2 mm) laminae, each composed of a fining upward sequence of quartz sand to yellow or gray clay. The repetitive nature of the sediments indicates a repetitive pattern of deposition, but whether it signifies a daily, seasonal, or yearly cycle cannot be determined. The method by which these laminae formed is also unclear. Finely laminated sediments are characteristic of sinkhole and cave deposits (Laury 1980; Agenbroad 1984; White et al. 1985). Milske et al. (1983) attributed deposition of laminated sediments in Mystery Cave, Minnesota, to variations in current velocity of the cave drainage system. At least two clay laminae in unit 5 contain well-preserved plant remains. These fossils are currently under study; however, preliminary analysis indicates that the remains are predominantly aquatic plants (Newsom pers. comm.).

Unit 5 is overlain by unit 6, a gray clay layer with numerous cobble- to pebble-size fragments of middle Crystal River limestone. Vertebrate fossils are numerous in the lower portion of this unit. Unit 6 grades upward into a somewhat less fossiliferous sandy-clay. Total thickness of unit 6 varies somewhat over the area excavated, ranging from 10 to 18 cm. Unit 7 is very similar to unit 6, and is composed of a clay-pebble layer that grades into a sand layer. Unit 7 is about 15 cm thick. The lowest portion of unit 8 is composed of clay-sand layers, rich in vertebrate fossils. In the upper level of unit 8, large limestone boulders are surrounded by fine sand.

Although there is no evidence of bioturbation of any of the layers and freshwater molluscs and ostracodes are absent, the laminated nature of the sediments, and the presence of aquatic plant remains indicate that the sand and clay sediments were water-lain. In addition, excavation revealed that bones and pebbles had caused deformation of the sediment layers, a phenomenon that occurs when sediments are wet or moist (Schrock 1948). Calcite structures previously interpreted as "dripstone" are also found in the most superficial layers of these units; however, these formations are probably of recent origin and are not speleothems.

4. Calcareous Sand Layers

The sediments above the boulder bar (Fig. 14) consist of several thick beds of limestone sand composed of breakdown products of the middle member of the Crystal River Formation (M. McKinney pers. comm.). The grains are not weathered, and the sand contains the characteristic forams *Lepidocylina* and *Operculinoides*. The layers above the upper boulder layer have been designated as units 12 through 17. Each of these beds is a massive lime-sand layer separated from the overlying unit by a thin clay lamina or a layer of calcite. Microfaunal remains are amazingly abundant and well-preserved in these layers, particularly in unit 15. A complete section of the layers above the boulder bar was exposed in a trench dug through the southern edge of the 5N,10E square. The total thickness of these layers exceeds 1.5 m, and the method by which they were formed is not known. However, based on the unique nature of these sediments when compared to the other sediment units of the site, it is clear that the environment of deposition changed after collapse of the final boulder layer.

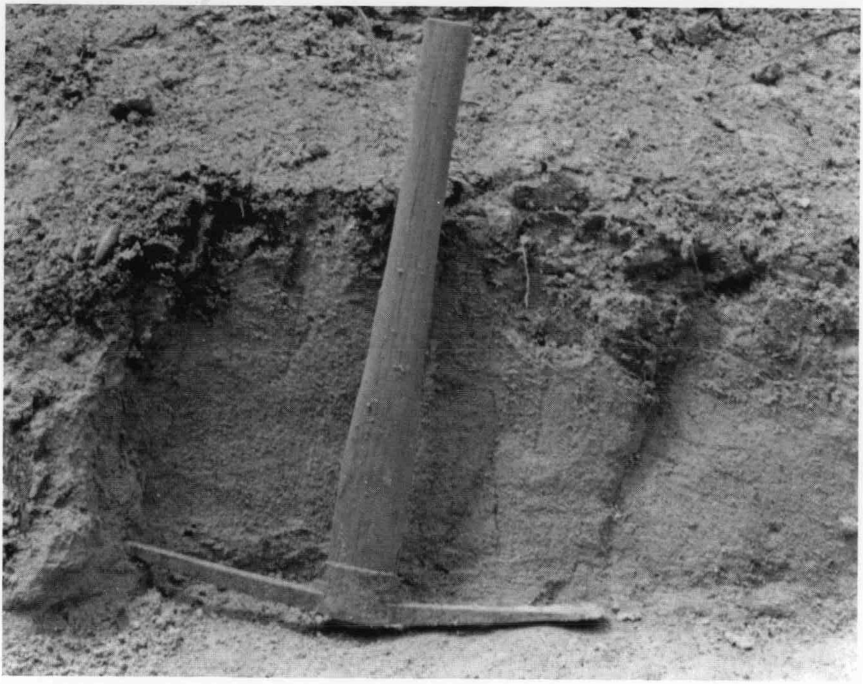

Figure 14. Vertical section showing massive calcareous sand layer unit 15. Length of pick handle = 42 cm.

Sediment Deposition and Site Formation: Summary

The features of the Thomas Farm sediments and associated limestone suggest that in the early Miocene, the site was a large sinkhole or cave. Although connection to surface drainage features such as above-ground streams is not indicated, it is likely that solution joints in the limestone provided internal or deep drainage, as is seen in present-day Florida sinkholes (Williams et al. 1977; Lane 1986).

The "sediment cone" formed as sediment, perhaps introduced from the ground surface above as well as entering the sinkhole through the underground drainage network, piled up on the floor of the sink. Sediments also formed from breakdown of the limestone itself. The presence of reworked fragments and fossils (i.e. *Chlamys spillmani*) of middle Crystal River age throughout the various layers of the site indicate that ground water was conducted through

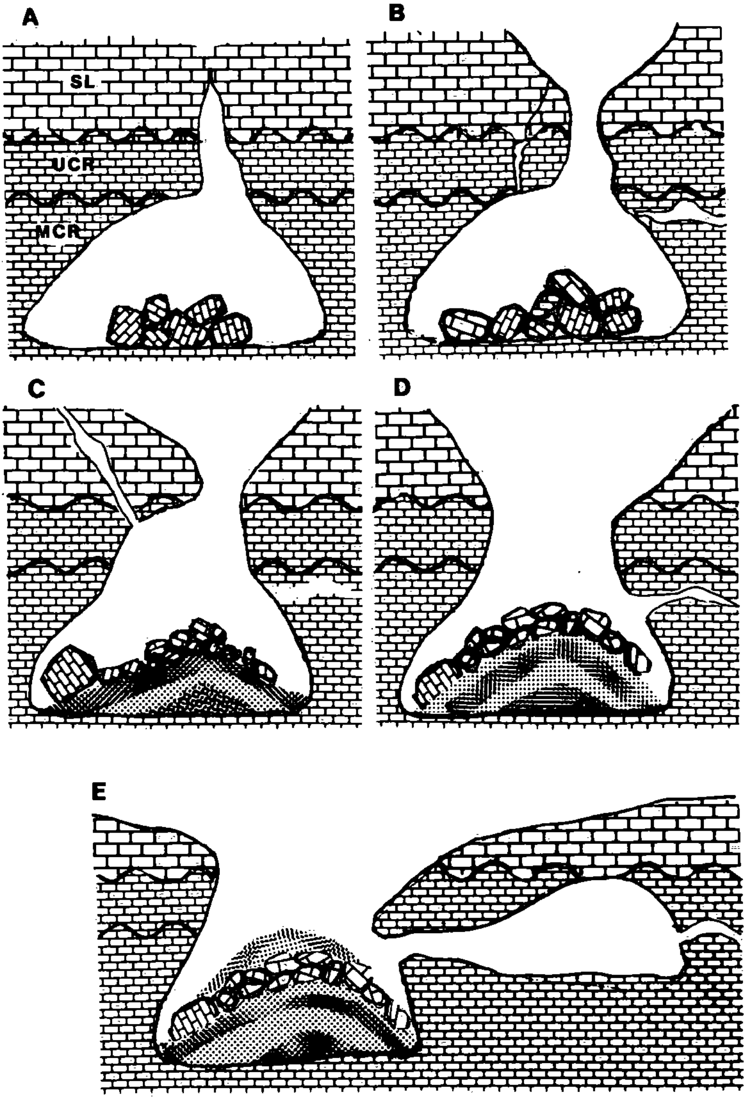

Figure 15. Proposed sequence of deposition at the Thomas Farm locality. (A) Formation of a chamber in middle Crystal River limestone. (B) Collapse of chamber roof forms base of debris cone. (C) Deposition of sands and clays, followed by wall collapse of upper Crystal River limestone (UCR). (D) Collapse of Suwannee Limestone (SL). (E) Formation of cave and deposition of calcareous sand outwash from cave onto debris cone.

solution joints in this limestone. Most artesian flow in north-central Florida today is carried through Crystal River limestones (Fergusen et al. 1947; Rosenau et al. 1977). The absence of speleothems from the fossiliferous clays and boulder layers suggests but does not necessarily prove that these sediments were not deposited in a cave. Caves in Florida that develop under certain environmental conditions (for example, water-filled caves) are not characterized by secondary calcite formations (Davis 1930; Lipchinsky 1963; Williams et al. 1977). If the sediments were deposited in a cave setting, it would appear that some agent must have transported bones to the locality, as will be discussed in the following section.

Although the exact mode of formation or deposition may never be known, Figure 15 presents a possible scenario of events important in the development and filling of Thomas Farm. Initial solution and collapse of limestone caused the formation of a chamber (or cave) within the limestone (A). With the subsequent collapse of the chamber roof, a sinkhole was formed, and deposition of bones and sediments began (B, C). The sinkhole is pictured in Figure 15 as jug-shaped, as this is a characteristic shape in early stages of formation of a collapse sinkhole. Early in the history of its development, the Thomas Farm sinkhole was water-filled, perhaps seasonally. The lower clay layers were water-lain. The sinkhole was fed and drained by underground drainage systems in the middle Crystal River Formation, possibly in response to fluctuating water table levels. Some event, perhaps partial collapse of a wall or overhang, caused a change in sediment input location and a shift in dip of beds. The first major collapse of upper Crystal River limestone (C) evidently occurred at a lower zone of weakness between it and the middle member of the Crystal River Formation and along the upper unconformity between the Crystal River and Suwannee Limestones (Cooke 1945; Puri and Vernon 1964). The huge boulders of upper Crystal River-age may also have fallen at this time. Shortly after the first collapse, the unsupported overhanging portion of Suwannee Limestone also broke apart and fell onto the debris cone (D). The reasons for the limestone collapse are not clearly known. One causal factor may have been lowered water table levels. Lowering of water levels may leave overhanging sections of limestone unsupported (Bogli 1980, Beck and Sinclair 1986; Lane 1986), which then break at zones of solution or weakness.

Massive calcareous sand layers mark the final stages of deposition of the Thomas Farm locality. The sedimentological and faunal differences between the upper sand units and the lower clay layers indicates that following the two major limestone collapse events, a major change in mode of deposition occurred. The fact that large numbers of microvertebrates, in particular bats, are present in these layers, and that the sand is composed of breakdown products of the middle Crystal River Formation, provide evidence that the upper sediments may have been outwash from a cave in the middle unit of the Crystal River Formation (E). It is clear that caves were present in the area prior to the major collapse event, as bat remains are found even in the lowest layers of the site; however, collapse of the sides of the sinkhole perhaps exposed the opening to a cave in the immediate vicinity of deposition. The cave was evidently frequented by mammalian and avian carnivores as well as bats (Pratt 1986, 1989). However, conditions no longer favored preservation of remains of large vertebrates.

The results of geological analysis indicate that several of the previously presented ideas concerning the mode of depositon of the Thomas Farm deposit are at least partially correct. This interpretation, based on additional data, presents a more complete view of site formation and shows that several of the depositional events were sequential rather than concurrent, as had been suggested by some earlier workers. Sedimentary evidence argues against the presence of a fluvial system of high competence. Taphonomic data compiled for the vertebrate fossils is presented in the next section and provides additional detailed information regarding the mechanisms by which the entire locality and bone concentrations formed.

Megafaunal Taphonomy

Taphonomic investigations are undertaken to determine the potential sources of a fossil concentration and the taphonomic factors that have acted to modify the assemblage. Features of the environment of deposition can also often be inferred by taphonomic analysis of the megavertebrate fossils found at a locality. Recent taphonomic studies (Korth 1979; Bown and Kraus 1981; Behrensmeyer 1982, 1988; Maas 1985; Badgley 1986a) have demonstrated that formation of bone concentrations, even in seemingly homogeneous environments of deposition, is an extremely complex process. Based on geologic evidence, Thomas Farm clearly represents some type of karst-related deposit, most likely a cave or sinkhole. Figure 16 lists possible mechanisms that may have been important both in forming the bone accumulation in a cave or sinkhole and in its further modification prior to excavation. The bone source within the sinkhole or cave was provided by animals either falling in or being transported in by some mechanism. A variety of agents such as weathering and scavenging potentially modified the assemblage prior to its recovery as a fossil deposit. In order to determine which events may have been crucial in the formation of the deposit, there are numerous aspects of a megavertebrate bone assemblage that may be examined from a taphonomic viewpoint. The four following areas of investigation have been shown in previous studies to provide the highest quality taphonomic information.

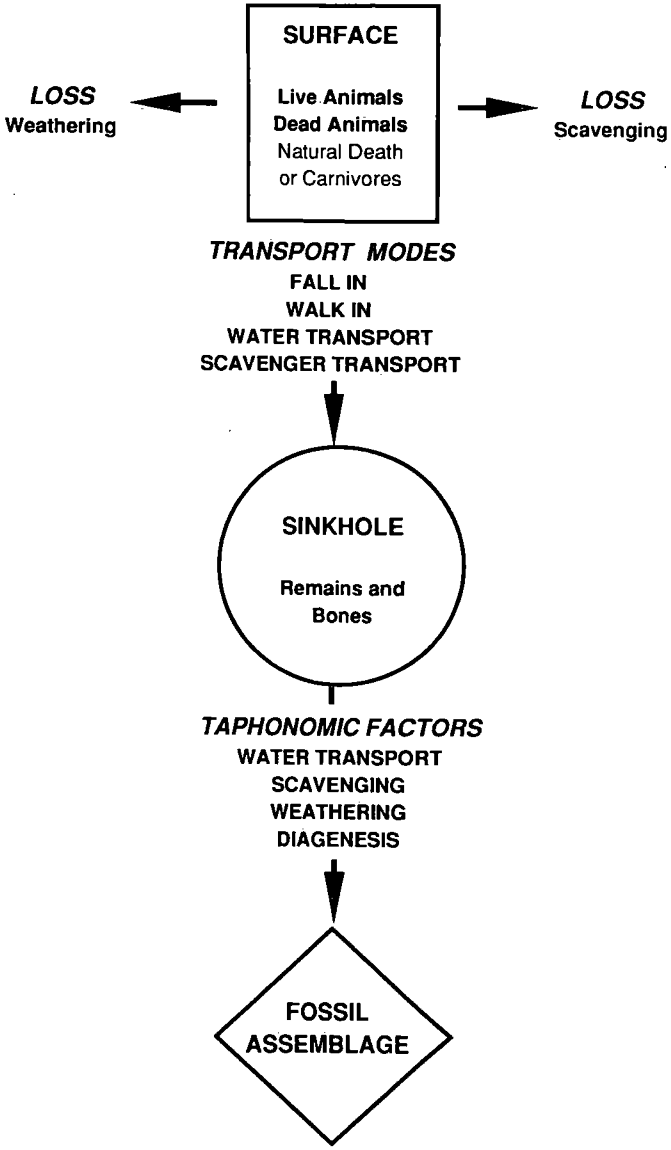

Figure 16. Summary of potential taphonomic pathways leading to formation of the Thomas Farm vertebrate fossil assemblage.

1. Surface features of the bones provide evidence of physical taphonomic factors such as weathering caused by subaerial exposure (Behrensmeyer 1975, 1978; Korth 1979; Andrews and Cook 1985), and abrasion characteristic of fluvially transported bone (Korth 1979; Shipman 1981; Shipman et al. 1981: Behrensmeyer 1982). Diagnostic breakage and surface modification may be caused by carnivores and scavengers (Bonnischen 1973; Haynes 1980, 1983; Hill 1980; Binford 1981) while other surface features are indicative of trampling (Andrews and Cook 1985; Behrensmeyer et al. 1986).
2. Faunal diversity and relative abundances of taxa provide information concerning the environment of deposition and possible sources of the bone concentration, in addition to indicating paleohabitats near the site of fossilization. In this study, comparison of faunal components between the various bone-bearing layers are made to determine if taphonomic, environmental, or depositional changes occurred during the course of site formation.
3. Activities that disperse or cause sorting of skeletal remains can be discerned by assessment of relative abundances of skeletal element types. Bones accumulated by carnivores and other biotic means often show recognizable patterns of representation (Behrensmeyer and Boaz 1980; Brain 1981; Binford 1981, Blumenschine 1986). High representations of hydrodynamically similar skeletal elements may indicate the presence of moving water and also provide estimates of minimum and maximum current speeds (Voorhies 1969; Behrensmeyer 1975; Korth 1979; Hanson 1980; Badgley 1986a).
4. Patterns of bone orientation can be extremely useful in taphonomic analysis (Voorhies 1969; Saunders 1977; Hunt 1978; Andrews et al. 1981; Shipman 1981; Shipman et al. 1981; Maas 1985). Observations on the presence of skeletal articulation or association as well as compass orientations of long bones and their positions within the enclosing sediment provide information concerning rates of burial, evidence of scavenging or trampling, and presence or absence of water-mediated transport.

Megafaunal vertebrate remains from the six most extensively excavated levels (units 5, 6, 7, 8, 11, and 15) are analyzed. Units 9 10, 12, 13, and 14 were the least fossiliferous layers and therefore were not extensively worked.

Types of Bone Modification

The physical condition of a fossil bone can provide information concerning taphonomic processes and depositional environment of a fossil locality. A bone may be altered both prior to its burial and after it has been buried and fossilized. The types of skeletal modification that occur after the animal's death and before the bone is either completely destroyed or buried provide documentation of events that occurred shortly after the death of the animal. Post-depositional changes are caused by processes that affect buried bone, either prior to or following its fossilization. Hill (1980) and Binford (1981) categorized types of post-mortem damage to bone. Types of destruction can also be grouped by causative taphonomic factors (Behrensmeyer 1978; Korth 1979; Pratt 1979; Binford 1981; Haynes 1980, 1983; Behrensmeyer et al. 1986).

A bone may be destroyed by weathering if it is exposed to climatic factors prior to its burial. Behrensmeyer (1978) documented six stages of weathering on Recent bone, ranging from stage 0 (no modification) to stage 5 (nearly complete breakdown). Bone destruction attributable to weathering provides evidence that the element was exposed on the ground surface before being covered by sediment. Within a fossil locality, recovery of elements exhibiting all stages of weathering indicates that the assemblage probably formed attritionally; however, even if the fossils do not appear to be weathered, an attritional assemblage cannot be ruled out. The degree of weathering is dependent on the type of climate, or even the microclimate at the ground surface, as well as the length of time of exposure (Behrensmeyer 1978). Bones that are exposed in the open prior to burial may also exhibit fine grooves and striations caused by roots and fungi (Haynes 1980; Andrews and Cook 1985).

Carnivores can be important agents of bone modification. Hill (1980) characterized the various types of damage attributable to predators; Bonnischen (1973), Binford (1981), Shipman (1981), and Haynes (1980, 1983), described bone destruction caused by various mammalian carnivores. Many of the diagnostic features are caused by a predator's teeth.

Large mammals can modify, damage, and even disperse skeletal elements by trampling them (Behrensmeyer and Boaz 1980; Andrews and Cook 1985; Behrensmeyer et al. 1986). Bones subject to trampling are characterized by diagnostic striations and, depending on the element, may be broken or crushed (Behrensmeyer and Boaz 1980).

Post-depositional damage, in particular breakage, is sometimes difficult to distinguish from pre-burial damage. The most diagnostic post-depositional break, a smooth stress fracture that occurs perpendicular to the long axis of the bone (Shipman 1981) is caused by sediment compaction. Bones may also be crushed by the weight of overlying sediments. Re-exposure of a bone, either prior to or following fossilization, also has the potential to cause modification and destruction. Water-worn or abraded bones are characteristic of fluvial environments. It is not the action of the water alone that causes bone destruction, but the waterborne sand particles that wear and polish the ends and processes of skeletal elements. The degree of water-wear on a bone is a function of the amount of time the element is exposed to the action of sand particles and the strength of the current involved. The bone may be modified as it is transported in an aquatic system or be abraded *in situ* as entrained particles move past (Behrensmeyer 1982). Therefore, this type of bone modification, while easily recognizable, is difficult to quantify. With the exception of a study by Korth (1979) on the effects of water-wear on microvertebrate remains, and observations by Shipman et al., (1981) and Behrensmeyer (1982), little quantitative information exists concerning the amount of abrasion seen on a bone and the length of time required to produce it. For the purposes of this study the degree of water-wear is assigned to four classes (Fig. 17). Unworn bone bears no obvious signs of water-wear. Minimal wear is indicated by slight rounding of ends of bones and processes and some pitting by sand grains on the surface of the bone. Moderately water-worn bone has rounded articular ends and processes, with cancellous bone visible at articular ends. The morphological features of the bone are still evident, so the bone is identifiable. Severely water-worn bone is characterized by completely abraded ends and processes. Distinguishing features have been obliterated.

Surface Modification of Thomas Farm Fossils

Compaction of sediments and repeated wetting and drying of the fossiliferous clays has caused extensive post-fossilization breakage of the Thomas Farm megavertebrate remains, as shown in Figure 18. Fossils near the present-day surface are subject to solution by ground water or are etched by root acids. These post-depositional factors have acted to obscure pre-fossilization features on a great number of the bones collected. Observations therefore pertain to bones that have been relatively undamaged by these events.

Unit 5. Vertebrate fossils recovered from unit 5 may be divided into two groups: those that show characteristic water-wear, and those that are unmodified. Complete elements, although not commonly found in this unit, show no signs of pre-burial destruction and, except for post-fossilization compaction breaks, are perfect. No bones found in unit 5 show signs of weathering, modification by carnivores, or trampling. Bones that have been abraded in running water are common and include both long bone fragments and epiphyses, podials, and phalanges. Water-wear ranges from minimal to

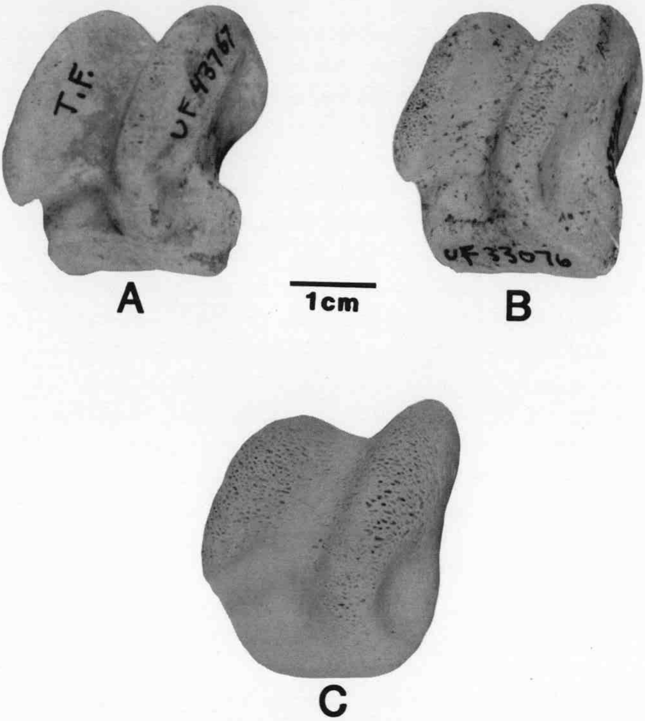

Figure 17. Bone water-wear classes, demonstrated on equid astragali. (A) Minimal wear, indicated by slight pitting of bone surface. (B) Moderate wear, characterized by early stages of surface abrasion and exposed cancellous bone. (C) Severe wear, indicated by high degree of rounding and by loss of distinguishing surface characteristics.

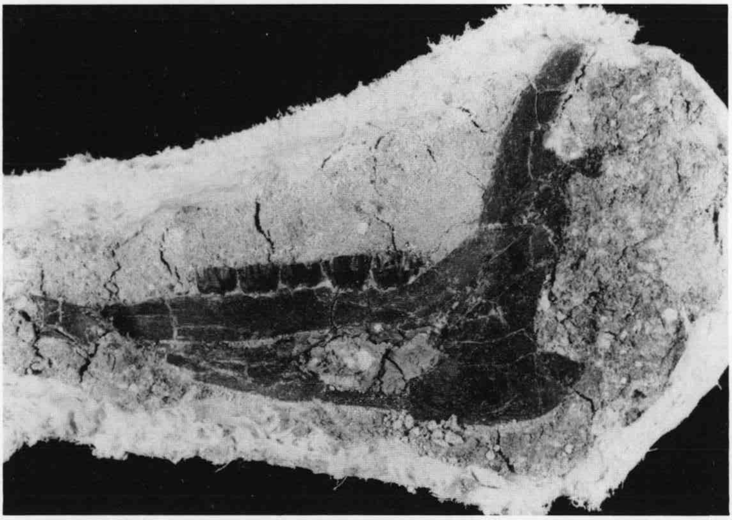

Figure 18. Partially prepared left dentary of *Parahippus leonensis*. Cracks are due to post-depositional compaction and sediment drying.

moderate, with podials showing the highest degree of abrasion. The presence of both complete, unaltered bones and of water-worn bones indicates that skeletal elements were derived from two sources. Complete bones may have been introduced into the sink from the immediate vicinity and buried rapidly, while the water-worn elements may have been transported to the sink from a more distant location. Alternately, the elements showing signs of water-wear may have simply been exposed, *in situ*, to sand abrasion. The lack of large quantities of severely abraded bones argues against the presence of a stream of high competence, and indicates that the water-worn bones were neither transported more than a few kilometers, nor exposed to abrasive sediments for any great length of time (Shipman et al. 1981; Behrensmeyer 1982).

Units 6 Through 8. Units 6 and 7 and the lower clay layer of unit 8 are very similar to one another in lithology and faunal content. Bones recovered from these beds show predominantly two types of destruction, weathering and water-wear, although the majority of the bones appear unmodified.

In unit 6, weathered elements are uncommon, and none of the bones collected shows evidence of climatic destruction beyond stage 1 of Behrensmeyer (1978), characterized by fine cracks running parallel to the long axis of the bone. The most notable alteration of the unit 6 fossils is abrasion caused by sand grains entrained in running water. Water-worn elements of the most numerous megafaunal species, *Parahippus leonensis* and *Archaeohippus blackbergi*, are common in unit 6. Roughly 66% of the podials, in particular scaphoids, lunars, and astragali, shows evidence of minimal to moderate water-wear. The larger bones show signs of wear at the articular ends, where the surface of the bone has been worn away to reveal the cancellous bone beneath. This feature may also be seen on the ends of weathered bones; however, the fossils have none of the other obvious characteristics (dessication cracks, flaking, etc.) associated with weathering. No evidence of bone destruction by trampling or by activities of carnivores was noted. Although carnivores regularly chew the ends of long bones, exposing cancellous portions (Bonnischen 1973; Haynes 1980, 1983; Binford 1981), this agent of destruction may be recognized by the jagged or uneven edges that result. The presence of water-worn bones in unit 6, as in unit 5, indicates that moving water was one of the taphonomic factors associated with the site during its formation.

Weathered bone is a more common feature of units 7 and 8 than of units 5 or 6, although bones from these upper layers do not show evidence of extreme weathering destruction. A small number of complete elements, in particular those found in unit 8, are more weathered on the side found facing upward in the deposit. Behrensmeyer (1978) noted that the surface of a bone that is facing upward is subject to greater climatic destruction than the side resting on the ground. The number of whole bones found with the more weathered surface upward may indicate that this type of modification occurred after the bones had attained their final resting positions and prior to immersion in water or burial, as exposure to air is a requirement for weathering. Therefore, the bottom of the sink may have been dry for an unknown period of time. The fact that the first sequence of limestone collapse took place shortly after deposition of this layer provides some support for this observation. Block collapse of limestone is reported to occur during dry or drought periods when water table levels are significantly lowered (Lane 1986). Small bones and bone fragments with weathered surfaces did not show any relationship between side found facing upward in the field and regions of heaviest weathering damage. It is possible that these bones were exposed subaerially elsewhere before falling into the sink, or were displaced by some agent, such as a scavenger or moving water, from their original positions within the sink.

Bone damage caused by carnivores is not apparent on fossils from units 7 and 8, with the exception of two elements of *Parahippus leonensis*. A depressed puncture hole, similar to that made by a mammalian carnivore canine (Haynes 1980, 1983; Hill 1980, Binford 1981; Shipman 1981) was found on a very damaged complete calcaneum from unit 7. The broken edge of a mandibular fragment from unit 8 has numerous depression fractures similar to those seen on chewed bone (Hill 1980; Binford 1981). The entire surfaces of both bones are pitted. It is possible that these two elements were initially derived from scat of a large mammalian carnivore. However, the rarity of bones with this type of modification implies that carnivores or scavengers did not have access to the majority of bones found in these layers.

Abrasion caused by water-wear is evident on a few elements from units 7 and 8. The astragalus, an element noticeably subject to fluvial abrasion, exhibits minimal to moderate water-wear in 3 of 5 specimens in unit 7, and on 1 of 14 specimens from unit 8. The bones obtained from the upper sand and boulder layer of unit 8 are often complete, although most have been crushed by post-depositional compaction. Little evidence of pre-burial climatic or biotic destruction can be discerned on these elements.

Unit 11. In unit 11, the upper boulder layer, large numbers of complete skeletal elements, including skulls and mandibles, are found. Unfortunately, the majority of the elements have been so crushed or deformed by post-depositional compaction that postmortem, pre-burial damage cannot be assessed. A few of the less damaged bones show weathering features equivalent to those of early stage 1 of Behrensmeyer (1978). Very little water-worn bone is found in this unit. Those bones that do show evidence of water-wear are very light in color, unlike the majority of darkly-colored bones found at the locality. The reason for this feature is not known, but does suggest a different taphonomic history for these elements.

No bones from unit 11 show signs of having been modified by trampling, and only a few show evidence of carnivore/scavenger activities. A complete horse innominate possesses several puncture holes probably caused by a small canid, but the rest of the bone is not damaged. A broken piece of a horse mandibular ramus has what appears to be a chewed edge as well as scoring marks on the surface (Binford 1981; Haynes 1983). However, the large number of complete bones present in unit 11 and the rarity of elements showing results of carnivore predation indicate that predators were involved only to a very minor extent in the accumulation of the mammalian remains found in the upper boulder layer.

Unit 15. Unit 15 is depauperate in megafauna and no complete limb bones of megafaunal taxa were recovered. Larger vertebrates are represented by long bone fragments, teeth, and footbones. As in unit 11, the few water-worn bones found in unit 15 are very light in color. Evidence of bone destruction by carnivores is most pronounced in this layer. A number of small bone fragments have chipped edges, a type of damage frequently caused by gnawing (Binford 1981), and several phalanges and distal calcanea possess puncture holes almost certainly caused by mammalian carnivores. As the microfaunal assemblage from unit 15 appears to be of scatological origin (Pratt 1986, 1989), it is likely that these small elements of megafaunal taxa were ingested by a predator.

Bone Modification--Summary

Results of the analysis of physical modification of Thomas Farm bones are summarized in Table 3. Although elements from the various layers show minor differences with regard to the types and degrees of modification, the overall dominant pattern is one of similarity.

In all units analyzed, weathering features are minimal. Lack of weathering may be explained in two ways. It is possible that most of the bones were never exposed to the forces of subaerial modification. If remains are buried shortly after the animal's death, as might occur in a catastrophic event (Behrensmeyer 1978), or if the carcass is immediately deposited into an aquatic system, the bones will not weather. Hill (1980) described the latter situation for Recent hippopotamus carcasses in a lake in the Amboseli National Park, Kenya. The floating carcasses were macerated by the lake waters, and the bones were presumably deposited on the lake floor. The alternate explanation is that Thomas Farm bones were exposed for some time in a terrestrial environment, but climatic conditions were not of sufficient severity to cause obvious weathering features. Behrensmeyer (1978) demonstrated that elements in wooded or moist environments are less likely to reach advanced weathering stages than bones exposed in open, arid areas. Andrews and Cook (1985) reported that bones of a Recent cow exposed in a temperate climate reached only stage 1 of weathering after 8 years, and Hill

Table 3. Types of surface modification of Thomas Farm fossils. Relative abundances of elements possessing features are assessed using the following scale: VR, very rare (less than 1%); R, rare (less than 10%); U, uncommon (less than 20%); C, common (30-50%); A, abundant (greater than 50%). Weathering stages range from 0 (unweathered) to 5 (severely weathered), as described in Behrensmeyer (1978). Degrees of water-wear are: Un, unmodified; Mn, minimal; Mo, moderate; and Se, severe. For a complete description of stages of water-wear see text and Figure 17.

MODIFICATION TYPE	SEDIMENTARY UNIT 5	6	7	8	11	15
Maximum Weathering Stage	0	1(R)	1(U)	1(U)	1(U)	-
Trampling Evidence	no	no	no	no	no	no
Carnivore Chew/Bite	no	no	VR	VR	VR	C
Water-wear Stage	Mn(C) Mo(U)	Mn(C) Mo(R)	Mn(U) Mo(U)	Mn(U)	Mn(VR)	Mn(VR)

(1980) noted that microclimatic factors and presence of protective vegetation may act to retard the weathering process. For these reasons, it cannot be definitely stated that Thomas Farm fossils showing no evidence of weathering were not subject to exposure, nor is it possible to estimate the length of time that bones showing evidence of weathering were exposed. The problem also remains as to whether these bones were modified *in situ*, or were introduced into the site from some other source. As discussed previously, it is likely that some of the bones from unit 8 were weathered in place, and it appears that the smaller weathered bones made their way into the deposit after laying out on the surface elsewhere.

The lack of both trampling marks and surface features indicative of actions of carnivores also suggest that the bones forming the assemblage were, in general, inaccessible to these agents of modification. Trampling of bones occurs in regions of "high traffic," such as trackways and watering holes (Behrensmeyer and Boaz 1980; Conybeare and Haynes 1984; Andrews and Cook 1985). Lack of trampling indicates that the sinkhole may have acted as a trap rather than as a watering hole. Bone assemblages modified by carnivores and scavengers fall into two general categories; kill sites and dens (Binford 1981), each of which may be recognized by particular taphonomic signatures. Bones taken to dens tend to be more heavily gnawed than are those abandoned at a kill site (Binford 1981). Haynes (1983) pointed out that the activities of carnivores and scavengers may not be indicated by gnawing, but as a rule other features, such as toothmarks or scrapes, will generally be present. The dearth of bones showing any evidence of carnivore activity and the absence of gnawed bones at Thomas Farm does not totally rule out the possibility that carcasses were disturbed or modified by carnivores and scavengers, but does suggest that the megavertebrate remains probably do not represent a den or lair accumulation.

The presence of water-worn bone, particularly in the lower sedimentary levels, indicates that these layers were associated with an aquatic environment and that current velocities were sufficient to cause transport and abrasion of the smaller elements. The fact that within the lower levels of the site the assemblage is a mixture of larger, unworn elements and smaller bones exhibiting features of water-wear suggests that the smaller elements may have been transported to the site from elsewhere and were deposited in the sinkhole as the current slowed. The lack of water-worn bone in the upper boulder layer, unit 11, suggests that the influence of moving water was less important in the later stages of site formation.

Faunal Composition

Species diversity and abundances of the vertebrate fauna represented at a fossil locality can provide evidence of factors responsible for formation of the bone assemblage. Only in rare cases, such as those involving catastrophic death and immediate burial do assemblages reflect living abundances of the living fauna. In most other instances the difference between fossil abundance and diversity and the diversity of the living fauna is due to any number of taphonomic factors.

Thomas Farm Faunal Composition

Relative abundances of taxa were estimated by two methods: by determining NISP (Badgley 1986a, 1986b), and by calculating the MNI per taxon (Shotwell 1955; Voorhies 1969; Wolff 1973; Grayson 1978; Damuth 1982). These abundance values do not reflect the relative abundances of the living taxa (Western 1980; Damuth 1982), and the values must be corrected if relative abundances of the once-living populations are to be estimated for paleoecological reconstruction. However, in taphonomic analysis, the abundance values provide a useful means of comparing the faunal compositions of the various sedimentary units. Relative abundances of megafaunal taxa in units 5, 6, 7, 8, 11, and 15 are shown in Table 4 and Figures 19 and 20. Values have been converted to percentages to facilitate comparisons between the sedimentary units.

The data demonstrate two major features of the Thomas Farm megafauna. Table 4 shows that sedimentary units 5 through 8 have a higher proportion of specimens of the aquatic taxa *Alligator olseni* and *Pseudemys* sp. than do the upper layers 11 and 15. Numbers of individuals of alligators are low because the specimens found (teeth and osteoderms) are not highly useful in MNI calculations. The presence of aquatic forms in the lower layers supports the sedimentological evidence that suggests these units were subject to water-mediated deposition. However, the relative rarity of aquatic turtles, both in abundance and number of species represented, contrasts dramatically with their great abundances in other aquatic sites in Florida, such as the McGeehee Farm (Rose and Weaver 1966; Jackson 1976), the Love Site (Webb et al. 1981), and the Leisey Shell Pit (Hulbert and Morgan 1989). Other components of the aquatic fauna well-represented at the above localities but virtually absent from Thomas Farm are bony fish. Fish are represented in the microfauna, but are extremely rare (Pratt 1986, 1989). The low representation of fish suggests that the water source at Thomas Farm was in some way isolated from aquatic environments such as surface streams and ponds, where fish are generally common in Florida. Laury (1980) attributed the relative rarity of fish at the Mammoth Springs site, South Dakota, to warmth of the water. Although thermal springs do occur in Florida today (Rosenau et al. 1977), water temperatures are not high enough to exclude fish. It is possible that high mineral content of the water might have caused conditions unsuitable for some aquatic organisms, but under such conditions it would be expected that all aquatic forms be absent. The presence not only of turtles and alligators but also of several species of presumably aquatic or semi-aquatic amphibians (Holman 1965, 1967; Estes 1963; Pratt 1986, 1989) suggests that this was not the case. It is intriguing that all aquatic or semi-aquatic members of the herpetofauna are capable of overland dispersal, and frequently make their way from one water source to another by this method (R. Franz pers. comm.).

A second obvious feature of the Thomas Farm megafauna is the numerical dominance of *Parahippus leonensis* in all but the uppermost sedimentary unit (Table 4). The high abundance of this species may reflect the animal's abundance in the area. Equids characteristically form herds, and Hulbert (1984) has suggested that the social structure of *P. leonensis* may have involved small herds. The site also may have attracted horses. Behrensmeyer and Boaz (1980) report that during periods of drought in the Amboseli Basin, Kenya, over 50% of the living mammalian megafauna in the vicinity of a water source is composed of migrating zebra and wildebeest. Although the Thomas Farm sinkhole may have served as a water source, to date there is no evidence that watering sites were rare or that the region was subject to prolonged drought.

The high abundances of *P. leonensis* also may be a function of the actions of taphonomic agents such as weathering, prey selection by carnivores, stream transport, or the trapping abilities of the site itself, which may cause a size bias

Table 4. Relative abundances of megafaunal species from the Thomas Farm locality. (A) Unit 5; (B) Unit 6; (C) Unit 7; (D) Unit 8; (E) Unit 11; and (F) Unit 15. See text for abbreviations.

Taxon	NISP	% of total	MNI	% of total
A. UNIT 5				
Chelonia (total)	27	6.3	5	19.3
Geochelone tedwhitei	13	3.0	2	7.7
Pseudemys sp.	14	3.3	3	11.6
Crocodylia				
Alligator olseni	180	41.7	3	11.6
Carnivora (total)	28	6.5	6	23.1
Amphicyon longiramus	2	0.5	1	3.8
Cynodesmus iamonensis or *Tomarctus canavus*	15	3.5	2	7.7
small canid	1	0.2	1	3.8
small mustelid	9	2.1	1	3.8
Hemicyon johnhenryi	1	0.2	1	3.8
Artiodactyla (total)	30	6.9	6	23.1
Nothokemas floridanus or *Floridatragulus dolicanthereus*	5	1.2	2	7.7
Prosynthetoceras texanus	2	0.5	1	3.8
Blastomeryx floridanus	15	3.5	2	7.7
Machaeromeryx gilchristensis	8	1.8	1	3.8
Perissodactyla (total)	166	38.5	7	26.9
Parahippus leonensis	112	25.9	3	11.4
Archaeohippus blackbergi	51	11.8	2	7.7
Anchitherium clarenci	2	0.5	1	3.8
Floridaceras whitei	1	0.2	1	3.8
Total Unit 5	431	100.0	26	100.0
B. UNIT 6				
Chelonia (total)	49	6.3	4	9.3
Geochelone tedwhitei	28	3.6	2	4.7
Pseudemys sp.	12	1.5	2	4.7
Unidentified	9	1.1	-	-
Crocodylia				
Alligator olseni	207	26.4	3	6.9

Table 4 Continued

Taxon	NISP	% of total	MNI	% of total
Carnivora (total)	58	7.4	10	23.3
Amphicyon longiramus	7	0.9	2	4.7
Cynelos caroniavorus	2	0.3	1	2.3
Cynodesmus iamonensis or *Tomarctus canavus*	36	4.5	2	4.7
small canid	2	0.3	1	2.3
Leptarctus ancipidens	4	0.5	2	4.7
small mustelid	5	0.6	1	2.3
Hemicyon johnhenryi	2	0.3	1	2.3
Artiodactyla (total)	83	10.6	9	20.9
Nothokemas floridanus or *Floridatragulus dolicanthereus*	9	1.1	2	4.7
Prosynthetoceras texanus	14	1.8	1	2.3
Blastomeryx floridanus	38	4.9	3	6.9
Machaeromeryx gilchristensis	21	2.7	2	4.7
Merycoidodon sp.	1	0.1	1	2.3
Perissodactyla (total)	387	49.4	17	39.5
Parahippus leonensis	253	32.3	9	20.9
Archaeohippus blackbergi	130	16.6	7	16.3
Floridaceras whitei	4	0.5	1	2.3
Total Unit 6	784	100.0	43	100.0
C. UNIT 7				
Chelonia (total)	46	6.4	4	12.1
Geochelone tedwhitei	20	2.8	2	6.1
Pseudemys sp.	12	1.7	2	6.1
Unidentified	14	1.9	-	-
Crocodylia				
Alligator olseni	136	18.9	3	9.1
Carnivora (total)	42	5.8	6	18.1
Amphicyon longiramus	5	0.7	1	3.0
Cynodesmus iamonensis or *Tomarctus canavus*	22	3.1	2	6.1
Leptarctus ancipidens	2	0.3	1	3.0
small mustelid	5	0.7	1	3.0
Hemicyon johnhenryi	1	0.1	1	3.0
Unidentified	7	1.0	-	-

Table 4 Continued

Taxon	NISP	% of total	MNI	% of total
Artiodactyla (total)	62	8.6	8	24.3
Nothokemas floridanus or *Floridatragulus dolicanthereus*	11	1.5	1	3.0
Prosynthetoceras texanus	19	2.6	3	9.1
Blastomeryx floridanus	22	3.1	2	6.1
Machaeromeryx gilchristensis	9	1.3	1	3.0
Desmathyus (?)	1	0.1	1	3.0
Perissodactyla (total)	435	60.3	12	36.4
Parahippus leonensis	288	39.9	5	15.2
Archaeohippus blackbergi	144	19.9	4	12.1
Anchitherium clarenci	1	0.1	1	3.0
Floridaceras whitei	1	0.1	1	3.0
Diceratherium barbouri	1	0.1	1	3.0
Total Unit 7	721	100.0	33	100.0
D. UNIT 8				
Chelonia (total)	34	6.0	3	8.8
Geochelone tedwhitei	17	3.0	2	5.8
Pseudemys sp.	10	1.8	1	2.9
Unidentified	7	1.2	-	-
Crocodylia				
Alligator olseni	45	7.9	2	5.8
Carnivora (total)	45	7.9	8	23.5
Amphicyon longiramus	3	0.5	1	2.9
Cynelos caroniavorus	4	0.7	1	2.9
Cynodesmus iamonensis or *Tomarctus canavus*	30	5.3	3	8.8
small canid	2	0.4	1	2.9
Leptarctus ancipidens	2	0.4	1	2.9
small mustelid	4	0.7	1	2.9
Artiodactyla (total)	86	15.2	9	26.5
Nothokemas floridanus or *Floridatragulus dolicanthereus*	39	6.8	3	8.8
Prosynthetoceras texanus	15	2.6	2	5.8
Blastomeryx floridanus	12	2.1	1	2.9
Machaeromeryx gilchristensis	18	3.2	2	5.8
Merycoidodon sp.	2	0.4	1	2.9

Table 4 Continued

Taxon	NISP	% of total	MNI	% of total
Perissodactyla (total)	356	62.9	12	35.3
Parahippus leonensis	276	48.7	7	20.6
Archaeohippus blackbergi	77	13.6	3	8.8
Anchitherium clarenci	2	0.4	1	2.9
Floridaceras whitei	1	0.2	1	2.9
Total Unit 8	566	100.0	34	100.0
E. UNIT 11				
Chelonia (total)	18	2.7	2	5.4
Geochelone tedwhitei	18	2.7	2	5.4
Crocodylia				
Alligator olseni	13	1.9	2	5.4
Carnivora (total)	67	10.2	9	24.3
Amphicyon longiramus	7	1.1	1	2.7
*Cynelos caroniavorus*8U	2	0.3	1	2.7
Cynodesmus iamonensis or *Tomarctus canavus*	25	3.8	3	8.1
small canid	1	0.2	1	2.7
Leptarctus ancipidens	2	0.3	1	2.7
small mustelid	7	1.1	1	2.7
Hemicyon johnhenryi	4	0.6	1	2.7
Unidentified	19	2.8	-	-
Artiodactyla (total)	79	12.0	9	24.3
Nothokemas floridanus or *Floridatragulus dolicanthereus*	42	6.4	3	8.1
large camelid	1	0.2	1	2.7
Prosynthetoceras texanus	11	1.7	2	5.4
Blastomeryx floridanus	8	1.2	1	2.7
Machaeromeryx gilchristensis	12	1.8	1	2.7
Desmathyus sp.	2	0.3	1	2.7
Unidentified	3	0.2	-	-
Perissodactyla (total)	481	73.1	15	40.5
Parahippus leonensis	350	53.2	9	24.3
Archaeohippus blackbergi	108	16.4	4	10.8
Anchitherium clarenci	2	0.3	1	2.7
Unidentified equid	19	2.8	-	-
Floridaceras whitei	2	0.3	1	2.7
Total Unit 11	658	100.0	37	100.0

Table 4 Continued

Taxon	NISP	% of total	MNI	% of total
F. UNIT 15				
Chelonia (total)	3	1.8	2	11.1
Geochelone tedwhitei	2	1.2	1	5.6
Pseudemys sp.	1	0.6	1	5.6
Crocodylia				
Alligator olseni	31	18.6	1	5.6
Carnivora (total)	28	16.9	7	38.8
Cynodesmus iamonensis or *Tomarctus canavus*	16	9.6	2	11.1
small canid	3	1.8	2	11.1
Leptarctus ancipidens	5	3.0	1	5.6
small mustelid	4	2.4	2	11.1
Artiodactyla (total)	41	24.7	5	27.7
Prosynthetoceras texanus	7	4.2	1	5.6
Blastomeryx floridanus	5	3.0	1	5.6
Machaeromeryx gilchristensis	29	17.5	3	16.7
Perissodactyla (total)	63	37.9	3	16.7
Parahippus leonensis	28	16.9	1	5.6
Archaeohippus blackbergi	35	21.1	2	11.1
Total Unit 15	166	100.0	18	100.0

in the fauna represented. Badgley (1986a) showed that size distributions within fossil faunas from the Siwaliks can be attributed in part to taphonomic factors. Table 5 shows body size distribution for the Thomas Farm megavertebrates.

A common feature of bone assemblages that form attritionally is the underrepresentation of small (less than 15 kg) taxa (Behrensmeyer et al. 1979; Behrensmeyer and Boaz 1980). Due primarily to higher birth and death rates (turnover), over a given period of time more small vertebrates die than larger vertebrates (Western 1980; Damuth 1982). However, loss of remains of small animals from a bone assemblage can be attributed to the greater effect of taphonomic agents on small bones with the highest surface area-to-volume ratios (Behrensmeyer et al. 1979; Behrensmeyer and Boaz 1980). Although

Table 5. Abundances of Thomas Farm mammals by size category. See Pratt (1986) for body mass estimates.

SEDIMENT LEVEL	BODY MASS (KG) 1-15 MNI	%	16-100 MNI	%	101-200 MNI	%	> 200 MNI	%
5	7	37	9	47	2	11	1	5
6	11	30	23	64	1	3	1	3
7	7	26	15	63	1	4	2	7
8	9	30	18	60	2	7	1	3
11	11	29	24	63	2	5	1	3
15	11	74	4	26	0	0	0	0

remains of small mammals at Thomas Farm are more poorly represented than those of mammals in the next largest size category, their abundance is considerably higher than that observed by Badgley (1986a) in a fluvial deposit from the Siwaliks in Pakistan. She proposed that low abundances of fossils in the 1-15 kg size range were due to winnowing of lighter elements by fluvial transport. The moderate representation of smaller vertebrates from Thomas Farm suggests that transport by moving water did not serve to dramatically decrease abundances of bones of smaller taxa.

Mammals in the 16-100 kg size category are the most highly represented at Thomas Farm, in part due to the fact that *P. leonensis* falls within this size range (Hulbert 1984). The high abundance of this form and others of similar size, and the relative rarity of larger mammals could be indicative of a predator-selected assemblage. Rosenzweig (1966) demonstrated the correlation between predator size and maximum prey size. Based on this relationship, the most likely predators of *P. leonensis* were the large carnivores *Hemicyon johnhenryi* and *Amphicyon longiramus* (Pratt 1986). Although this hypothesis will be examined further in a later section, based on the rarity of bone showing evidence of carnivore modification, it is unlikely that carnivores were the sole or major contributors to the bone accumulation.

It is also possible that the site itself acted as a size-selective trap. The low representation of larger members of the fauna (over 100 kg) may indicate that they were too large to have gained access to the sinkhole, although this hypothesis is not supported by evidence on skeletal dispersal (see following section). The significance of the composition of the Thomas Farm megafauna awaits future discoveries of other early Miocene localities from Florida with which this fauna may be compared. The high representation of *P. leonensis* and lower representations of larger mammals cannot be fully explained at this time.

Although it is not possible to compare the Thomas Farm fauna with other Florida faunas of similar age, comparison of faunal composition from the various layers of the site itself can provide evidence both of changes in environment and of taphonomic events that occurred during the course of deposition. Comparisons of faunal abundances in the lower sand and clay units show that relative abundances of taxa in unit 5 are different from those of units 6, 7, and 8 (Figs. 19 and 20). Alligator specimens are higher in relative abundance and equid remains are lower in relative abundance in unit 5 compared to units 6 though 8. Units 6 through 11 appear generally similar in terms of relative NISP per taxon, while values for unit 15 are clearly different from those of other layers (Fig. 19). If relative NISP per taxon from each layer are compared statistically with those of other layers using the R x C test of independence using the *G*-test (Sokal and Rohlf 1981), relative abundances in each unit, except 6 and 7, are significantly different from those in the over-lying and under-lying units at the $p = 0.01$ level (Table 6).

If relative abundances in terms of MNI per taxon per sedimentary level are compared (Fig. 20), the differences in relative abundances of taxa between the units are minimized. The main reason for the apparent increase in similarity of different levels if MNI rather than NISP are used is caused by species that possess large numbers of elements that are not diagnostic in MNI calculations (for example, alligator). Application of a R x C analysis of independence using the *G*-test (Sokal and Rohlf 1981) shows that in terms of relative MNI per order of megafaunal taxa, no sedimentary unit, with the exception of level 15, is significantly different from the one above or below it at the $p = .01$ level (Table 6).

Badgley (1986a, 1986b) discussed the relative merits of NISP and MNI calculations, and the circumstances under which each should be employed. It is obvious that for the Thomas Farm fauna, NISP overestimates the differences between levels, and MNI underestimates these differences. Nevertheless, both methods indicate that in terms of fauna preserved, the factors governing formation of the bone assemblage were fairly constant until deposition of the final layer, unit 15. The fact that the same species are represented in all units of the site indicates that neither a dramatic change in climate, environment, nor the vertebrate fauna took place during the period of time the site was sampling the fauna.

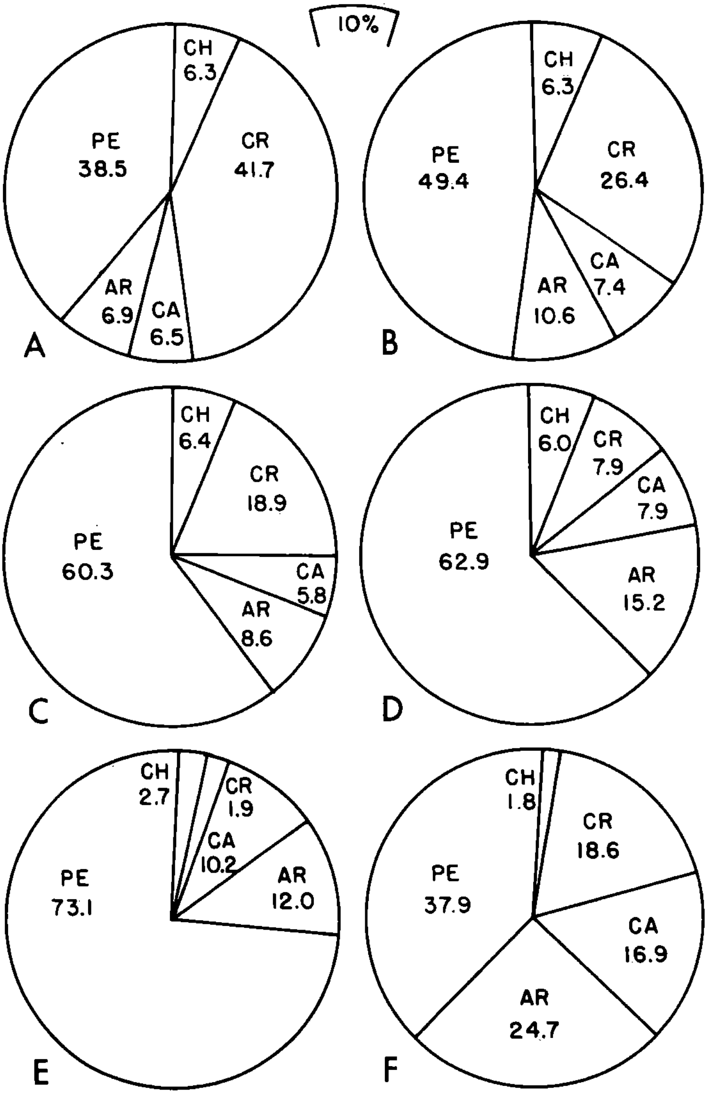

Figure 19. Relative abundances of identifiable specimens per order of megafaunal taxa. (A) Unit 5. (B) Unit 6. (C) Unit 7. (D) Unit 8. (E) Unit 11. (F) Unit 15. Abbreviations: AR, Artiodactyla; CA, Carnivora; CH, Chelonia; CR, Crocodilia; PE, Perissodactyla.

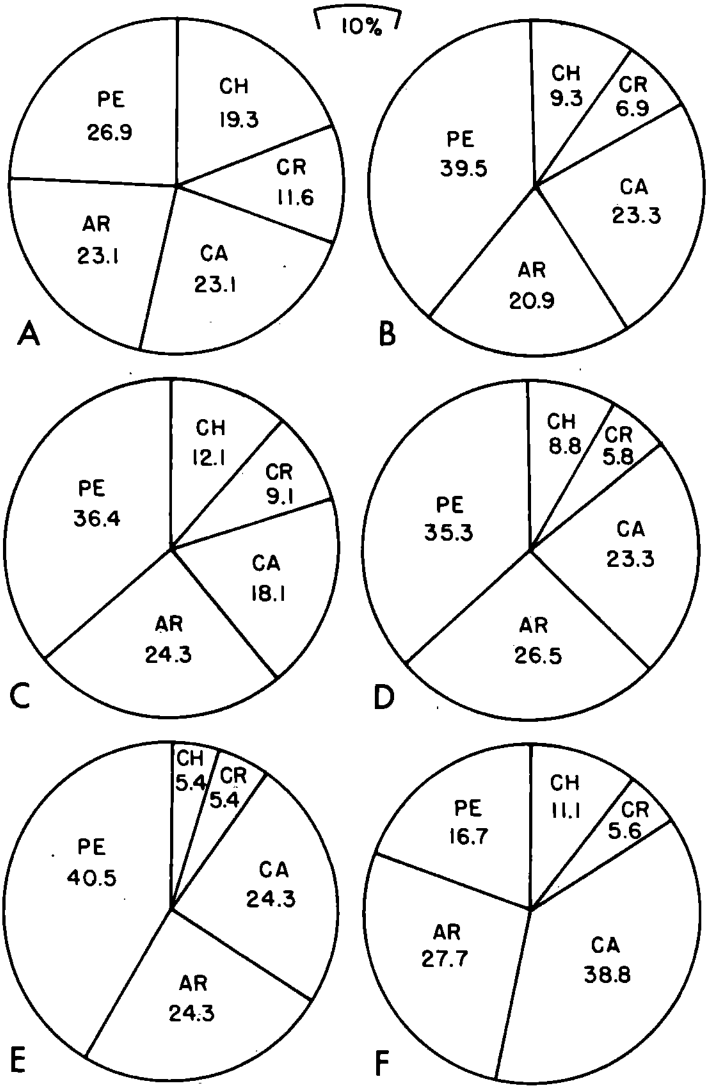

Figure 20. Relative abundances of minimum numbers of individuals (MNI) per order of megafaunal taxa. (A) Unit 5. (B) Unit 6. (C) Unit 7. (D) Unit 8. (E) Unit 11. (F) Unit 15. See Figure 19 for list of abbreviations.

Table 6. Statistical comparison of relative abundances of megafaunal taxa from different sedimentary units at Thomas Farm, based on (a) NISP and (b) MNI. Reported are calculated *G* values from the R x C test for association (Sokal and Rohlf 1981:599). Abundance values are considered significantly different at the 0.01 level if *G* > 13.28 at 4 degrees of freedom (*). For explanation of test and abbreviations see text.

Unit	6	7	8	11	15
5 (a)	*27.5	-	-	-	-
(b)	1.1	-	-	-	-
6 (a)		10.3	-	-	-
(b)		0.2	-	-	-
7 (a)			*21.5	-	-
(b)			0.8	-	-
8 (a)				*20.1	-
(b)				0.3	-
11 (a)					*49.3
(b)					2.0

Skeletal Articulation or Association

The extent of articulation of vertebrate skeletal remains provides insight into the method by which bones have accumulated and the possible span of time involved in the formation of the assemblage. Completely articulated skeletons are rare in the fossil record, and generally indicate that only a short time had elapsed between death and burial, such that the remains were not greatly modified or dispersed by taphonomic events. If articulated remains are not present, then the abundances of bones and their positions within the sediment have the potential to provide clues concerning the taphonomic factors important in forming and modifying the assemblage.

Thomas Farm Skeletal Asssociations

Figures 21A and 21B, depicting locations of fossil bones within two representative square meters of Thomas Farm, clearly show that megafaunal remains are not articulated. Bones of *Parahippus leonensis* are extremely abundant, and it is assumed that at least some of these elements were from associated skeletons. However, with the exception of a femur and tibia and an astragalus and calcaneum, no definite articular matches could be made. Efforts to match postcranial elements of a single individual were hampered not only by the large number of *P. leonensis* elements found in every square excavated, but also by the fact that many bones were deformed or crushed by post-depositional compaction. Bones of taxa that are relatively rare, such as

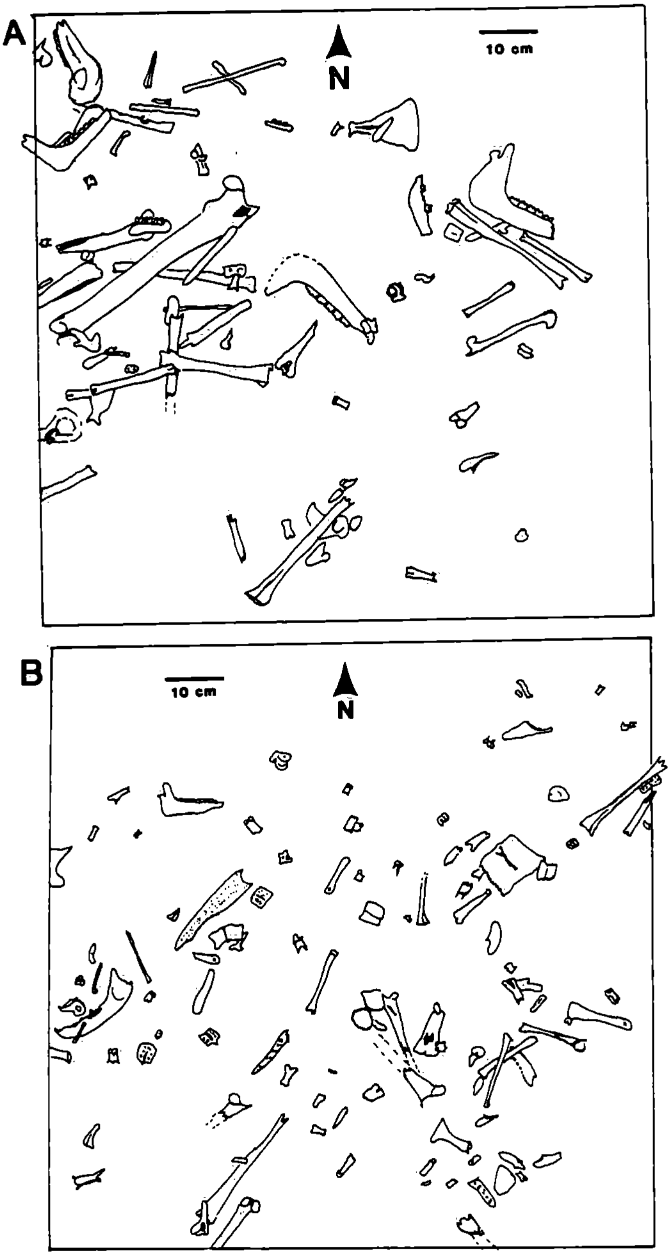

Figure 21. Bone plots of representative square meters at Thomas Farm. (A) 10N x 10E, M11, unit 11. (B) 15N x 10E, M20, unit 6.

rhinoceros and amphicyonid, do seem to be concentrated in areal extent within certain layers, suggesting the possibility that these elements may be parts of the same skeleton. However, to date no strong evidence (such as an articular match between elements) has been found to suggest that these elements were all derived from one individual. Behrensmeyer and Hill (1984) have suggested that even in the absence of articulation, associations of skeletal parts may be indicated by the similar, high relative abundances of elements that disarticulate late in the disarticulation sequence. However, as sequences of disarticulation vary considerably depending on the type of animal and the environment (arid, moist, aquatic) in which decomposition occurs, this method cannot be used to indicate association of *P. leonensis*.

Among the lower vertebrates, evidence of skeletal association is rare. Turtle and tortoise shells are almost always disarticulated. With the exception of two portions of a broken pleural bone found several meters apart within the same sedimentary layer, no matches were found between disarticulated parts of chelonian shells. Kenneth Dodd (pers. comm.) has noted that shells of aquatic turtles disarticulate completely within 8 months when exposed in modern Florida terrestrial environments, and presumably less time is required for disarticulation under aquatic conditions, assuming the shells are not buried.

The conclusion drawn from the absence of articulated skeletons is that burial of the megafaunal remains at Thomas Farm was not taking place under conditions that favor the preservation of complete skeletons. Therefore, events related to disarticulation of skeletons and modification of the bone concentration were undoubtedly responsible for biasing bone representations within the assemblage.

Element Representation

Representation assessments of skeletal elements provide an estimate of the relative abundance of each element type recovered from a fossil deposit. Given that taphonomic factors may bias a bone assemblage by leading to increases or deceases in bone abundances of the original death assemblage, it is hypothetically possible to recognize causative taphonomic agents by patterns of skeletal element abundance. Any combination of the events listed in Figure 16 may have been responsible for the final assemblage, and therefore representation patterns of bones may be correspondingly complex (Behrensmeyer 1982; 1988). However, if one taphonomic agent was of overriding importance, then the composition of the fossil bone assemblage may record this fact. For this reason, comparisons of bone relative abundances in a fossil assemblage with those in Recent bone accumulations of known origin can serve to indicate possible factors involved in modifying the fossil assemblage.

In this study, the Thomas Farm assemblage was compared with modern bone accumulations, listed below, that were formed or modified by taphonomic agents similar to those proposed to have been involved in the formation of the Thomas Farm deposit (Fig. 16):

1. Attritional death assemblage: Behrensmeyer and Boaz (1980) recorded bone abundances for a large collection of carcasses in the Amboseli National Park, Kenya. The assemblage, formed primarily of mammals dying of natural causes, was modified to some extent by carnivores and scavengers, trampling, and weathering. This impressive body of data provides a representative example of the ways in which a death assemblage, exposed on the ground surface, can be modified in terms of bone representation.
2. Carnivore kill site: Areas where animals congregate, such as watering holes, are often sites where predators stalk and kill prey. After feeding, carnivores may abandon bones at these locations (Binford 1981). Although bone representations vary due to a large number of factors such as type of predator, size and age of prey, and time of year (Binford 1981; Blumenschine 1986), a kill site assemblage often possesses a diagnostic pattern of element representation (Behrensmeyer and Boaz 1980; Binford 1981; Blumenschine 1986). Records of Recent bone assemblages formed in this manner include a study by Binford (1981) on remains of caribou killed by wolves, and Hill's data (from Binford 1981) on skeletal abundances of topi killed by a variety of predators. Although other studies on bone assemblages formed by carnivores are known (e.g. Blumenschine 1986), the two examples cited here are considered most suitable for several reasons. Thomas Farm carnivores capable of killing large prey, such as *Parahippus leonensis*, include two species of canid, two species of amphicyonid, and an ursid. Several of these taxa are very wolf-like in their morphology (Pratt 1986). Although caribou are considerably larger than *P. leonensis*, topi, with an average body mass of about 80 kg (Binford 1981), are within the proposed size range of the fossil horse species (Hulbert 1984). Finally, these Recent samples provide quantitative bone counts against which fossil bone abundances may be easily compared.
3. Carnivore den or lair: Predators and scavengers may remove portions of a carcass from the scene of a kill and transport them to their living quarters. Accumulations of bones formed

in this way by wolves (Binford 1981) and hyaenas (Behrensmeyer and Boaz 1980) are compared with the fossil accumulation.

4. Moving water: Bones may be added to or removed from an accumulation by the action of moving water. An assemblage consisting of elements that may have either resisted transport or been carried from elsewhere, may be recognized by the numbers and types of bones present. Voorhies (1969) established transport groups for bones of the mammalian skeleton by demonstrating that certain bone types behave in a similar fashion in running water. Behrensmeyer (1975) showed that the ability of a bone to be moved or resist transport can be assessed quantitatively by treating the element as a sedimentary particle. Hanson (1980) suggested that the role of moving water in forming and modifying an assemblage may be evaluated by comparing relative abundances of bones from each of the various transport groups. A generalized transport sequence for bones of *Parahippus leonensis* based on previous studies (Voorhies 1969; Behrensmeyer 1975; Korth 1979; Pratt 1979), stream experiments conducted in association with this study, and estimations of quartz grain equivalents, is shown in Table 7.

Element Representation at Thomas Farm

Relative abundances of skeletal elements may be assessed by two different methods. The first, skeletal-part frequency (Badgley 1986a), refers to the percentage of the total bone assemblage represented by each element type (Table 8). Comparison with the percentage frequency of the same element in a complete skeleton indicates which fossil bones are present in higher or lower proportions than expected in an unmodified death assemblage. Obviously, the greatest differences in terms of percentage representation between a fossil assemblage and a complete skeleton are likely to be seen in elements such as vertebrae, teeth, and phalanges that possess the highest skeletal-part frequency values in a living mammal. Conversely, lowest differences between fossil and recent assemblages in terms of skeletal-part percentages tend to be elements such as skulls that are represented by only one element in the complete skeleton.

An alternative method of quantifying skeletal element abundance involves dividing the number of each fossil element type present by the number expected based on the MNI (Wolff 1963; Voorhies 1969; Korth 1979), to arrive at a percentage value termed the relative representation (Table 8). In actuality, this number reflects the abundance of each bone type relative to the most abundant element. If factors have acted to cause the enrichment of one element in the assemblage, then representation values of other elements may appear deceptively low. Although each method of calculating bone abundances has certain shortcomings, use of the two methods together provides the most informative picture of bone representation patterns. In the comparison of abundances of fossil bones with those in a modern accumulation, differences in relative abundances of individual bone types are to be expected, and should not be weighted too heavily. Rather, similarities or differences in overall abundance patterns provide more information in comparing Recent and fossil assemblages. The analysis of element preservation at the Thomas Farm locality was restricted to elements of *Parahippus leonensis* for several reasons. *P. leonensis* is the most abundant member of the larger (over 5 kg) mammalian fauna at the locality, and its easily identifiable remains are found in all of the major units. Because it is difficult to assign many of the postcranial elements of the Thomas Farm carnivores and artiodactyls to species, MNI calculations for each species of these groups must be based on cranial material, and relative representations of elements cannot be determined. In addition, the size range of *P. leonensis* is small (Hulbert 1984), so that in consideration of fluvial transport groups, effects of size variations within element types need not be considered.

Unit 5. Table 8 lists skeletal part frequencies and relative representations of *Parahippus leonensis* elements recovered from unit 5. Differences in frequency values between unit 5 elements and those of a complete skeleton are

Table 7. Predicted transport groups for elements of *Parahippus leonensis*. Arrows indicate elements that due to shape, or differences in wet and dry densities, may belong to more than one dispersal group. Range of calculated quartz grain equivalent diameters listed in parentheses. See text for discussion of quartz grain equivalents.

Transport Group			
(<3 mm) I	(>3 mm) I/II	(>10 mm) II	(>20 mm) II/III & III
small podials	cheekteeth	humerus	dentary
phalanges	incisors	radius	←---skull
vertebrae	astragalus	←---femur	
ribs	calcaneum	tibia	
l. metapodial	prox. ulna	←---pelvis---→	
	←---large podials	m. metapodial	
		←---scapula	
		petrosal	

Table 8. Relative abundances of elements of *Parahippus leonensis* from major sedimentary units of the Thomas Farm locality. Abbreviations: No., number of each element; Rl. rep, percent relative representation; S-PF, skeletal-part frequency; Ectocun., ectocuneiform; Entocun., entocuneiform; Mesoentocun., mesoentocuneiform; D., distal; M., medial; Pr., proximal. See text for discussion of calculations.

	UNIT 5 MNI=3			UNIT 6 MNI=9		
ELEMENT	No.	S-PF	Rl. rep	No.	S-PF	Rl. Rep
Maxilla	0	0	0	0	0	0
Dentary	3	0.027	50.0	5	0.021	27.7
Incisor	8	0.071	22.2	7	0.030	6.5
Cheektooth	18	0.161	25.0	17	0.043	7.8
Scapula	1	0.009	16.7	4	0.017	22.2
Humerus	1	0.009	16.7	7	0.030	38.9
Radius	4	0.035	66.7	4	0.017	22.2
Ulna	2	0.018	33.3	4	0.017	22.2
Scaphoid	2	0.018	33.3	4	0.017	22.2
Cuneiform	2	0.018	33.3	2	0.008	11.1
Pisiform	1	0.009	16.7	4	0.017	22.2
Magnum	1	0.009	16.7	5	0.021	27.8
Lunar	0	0	0	2	0.008	11.1
Unciform	1	0.009	16.7	6	0.026	33.3
Trapezium	0	0	0	1	0.004	5.6
Metacarpal III	4	0.035	66.7	1	0.004	5.6
Innominate	3	0.027	50.0	4	0.017	22.2
Femur	2	0.018	33.3	5	0.021	27.8
Patella	1	0.009	16.7	5	0.021	27.8
Tibia	2	0.018	33.3	11	0.047	61.1
Calcaneum	0	0	0	12	0.052	66.7
Astragalus	1	0.009	16.7	6	0.026	33.3
Navicular	2	0.018	33.3	7	0.030	38.9
Cuboid	1	0.009	16.7	4	0.017	22.2
Entocun.	2	0.018	33.3	2	0.008	11.1
Mesoentocun.	0	0	0	1	0.004	5.6
Ectocun.	2	0.018	33.3	1	0.004	5.6
Metatarsal III	0	0	0	3	0.013	16.7
Lateral Metatarsal	10	0.089	41.7	15	0.065	20.8
Pr. Phalanx III	4	0.035	33.3	16	0.070	44.4
M. Phalanx III	4	0.035	33.3	15	0.065	41.7
D. Phalanx III	0	0	0	3	0.013	8.3
Pr. Lateral Phalanx	12	0.107	50.0	11	0.047	15.3
M. Lateral Phalanx	5	0.045	20.8	6	0.026	8.3
D. Lateral Phalanx	4	0.035	16.7	3	0.013	4.2
Vertebra	9	0.080	7.2	30	0.131	7.9
TOTAL	112			228		

Table 8 Continued

	UNIT 7 MNI= 5			UNIT 8 MNI= 7		
ELEMENT	No.	S-PF	Rl. rep	No.	S-PF	Rl. Rep
Maxilla	0	0	0	1	0.004	14.3
Dentary	4	0.014	40.0	9	0.033	64.3
Incisor	13	0.046	21.6	7	0.025	8.3
Cheektooth	52	0.183	43.3	35	0.127	20.8
Scapula	2	0.007	20.0	0	0	0
Humerus	4	0.014	40.0	11	0.040	78.5
Radius	5	0.018	50.0	10	0.036	71.4
Ulna	5	0.018	50.0	8	0.029	57.1
Scaphoid	9	0.032	90.0	10	0.036	71.4
Cuneiform	3	0.010	30.0	2	0.007	14.3
Pisiform	4	0.014	40.0	1	0.004	7.1
Magnum	7	0.025	70.0	2	0.007	14.3
Lunar	3	0.010	30.0	3	0.011	21.4
Unciform	7	0.025	70.0	2	0.007	14.3
Trapezium	1	0.003	10.0	2	0.007	14.3
Metacarpal III	7	0.025	70.0	2	0.007	14.3
Innominate	4	0.014	40.0	4	0.014	28.6
Femur	5	0.018	50.0	5	0.018	35.7
Patella	1	0.003	10.0	6	0.022	42.8
Tibia	7	0.025	70.0	8	0.029	57.1
Calcaneum	6	0.021	60.0	9	0.032	64.3
Astragalus	5	0.018	50.0	14	0.051	100.0
Navicular	4	0.014	40.0	10	0.036	71.4
Cuboid	9	0.032	90.0	5	0.018	35.7
Entocun.	0	0	0	0	0	0
Mesoentocun.	5	0.018	50.0	0	0	0
Ectocun.	1	0.003	10.0	3	0.011	21.4
Metatarsal III	5	0.018	50.0	2	0.007	14.2
Lateral Metatarsal	18	0.063	55.0	14	0.051	25.0
Pr. Phalanx III	13	0.046	65.0	22	0.080	78.6
M. Phalanx III	15	0.053	75.0	8	0.029	28.6
D. Phalanx III	6	0.021	30.0	4	0.014	14.3
Pr. Lateral Phalanx	19	0.067	47.5	15	0.054	26.8
M. Lateral Phalanx	12	0.042	30.0	4	0.014	7.1
D. Lateral Phalanx	1	0.003	2.5	3	0.011	5.3
Vertebra	22	0.077	10.5	35	0.127	11.9
TOTAL	284			276		

Table 8 Continued

	UNIT 6-8 MNI = 17			UNIT 11 MNI = 9		
ELEMENT	No.	S-PF	Rl. rep	No.	S-PF	Rl. Rep
Maxilla	1	0.001	2.9	2	0.006	11.1
Dentary	18	0.023	52.9	10	0.029	55.6
Incisor	27	0.034	13.2	20	0.058	18.5
Cheektooth	104	0.131	25.5	78	0.225	36.1
Scapula	6	0.007	17.6	6	0.017	33.3
Humerus	22	0.028	64.7	8	0.023	44.4
Radius	19	0.024	55.8	7	0.020	39.0
Ulna	17	0.021	50.0	8	0.023	44.4
Scaphoid	23	0.029	67.6	3	0.009	16.7
Cuneiform	7	0.009	20.5	0	0	0
Pisiform	9	0.011	26.4	3	0.009	16.7
Magnum	14	0.018	41.2	4	0.012	22.2
Lunar	8	0.010	23.5	3	0.009	16.7
Unciform	15	0.019	44.1	0	0	0
Trapezium	4	0.005	11.7	0	0	0
Metacarpal III	10	0.013	29.4	9	0.026	50.0
Innominate	12	0.015	35.3	8	0.023	44.4
Femur	15	0.019	44.1	11	0.032	61.1
Patella	12	0.015	35.3	4	0.012	22.2
Tibia	26	0.033	76.5	16	0.046	88.9
Calcaneum	27	0.034	79.4	10	0.029	55.6
Astragalus	25	0.032	73.5	8	0.023	44.4
Navicular	21	0.026	61.7	6	0.017	33.3
Cuboid	18	0.022	52.9	4	0.012	22.2
Mesoentocun.	6	0.007	17.6	0	0	0
Entocun.	2	0.003	5.9	0	0	
Ectocun.	5	0.006	14.7	8	0.023	44.4
Metatarsal III	10	0.013	29.4	7	0.020	38.8
Lateral Metatarsal	47	0.059	34.5	23	0.066	32.0
Pr. Phalanx III	51	0.064	75.0	7	0.020	19.4
M. Phalanx III	38	0.048	55.5	12	0.035	33.3
D. Phalanx III	13	0.016	19.2	2	0.006	5.5
Pr. Lateral Phalanx	45	0.057	33.1	18	0.052	25.0
M. Lateral Phalanx	22	0.028	16.1	4	0.012	5.5
D. Lateral Phalanx	7	0.009	5.1	1	0.003	1.4
Vertebra	87	0.110	12.2	37	0.107	9.7
TOTAL	793			346		

Table 8 Continued

	UNIT 15 MNI = 1			COMPLETE SKELETON	
ELEMENT	No.	S-PF	Rl. rep	No.	S-PF
Maxilla	0	0	0	2	0.011
Dentary	1	0.042	50.0	2	0.011
Incisor	4	0.167	33.3	12	0.069
Cheektooth	2	0.083	8.3	24	0.138
Scapula	0	0	0	2	0.011
Humerus	1	0.042	50.0	2	0.011
Radius	0	0	0	2	0.011
Ulna	0	0	0	2	0.011
Scaphoid	0	0	0	2	0.011
Cuneiform	1	0.042	50.0	2	0.011
Pisiform	1	0.042	50.0	2	0.011
Magnum	0	0	0	2	0.011
Lunar	0	0	0	2	0.011
Unciform	0	0	0	2	0.011
Trapezium	0	0	0	2	0.011
Metacarpal III	0	0	0	2	0.011
Innominate	1	0.042	50.0	2	0.011
Femur	1	0.042	50.0	2	0.011
Patella	0	0	0	2	0.011
Tibia	0	0	0	2	0.011
Calcaneum	0	0	0	2	0.011
Astragalus	0	0	0	2	0.011
Navicular	1	0.042	50.0	2	0.011
Cuboid	0	0	0	2	0.011
Mesoentocun.	0	0	0	2	0.011
Entocun.	0	0	0	2	0.011
Ectocun.	0	0	0	2	0.011
Metatarsal III	0	0	0	2	0.011
Lateral Metatarsal	0	0	0	8	0.046
Pr. Phalanx III	1	0.042	25.0	4	0.023
M. Phalanx III	0	0	0	4	0.023
D. Phalanx III	1	0.042	25.0	4	0.023
Pr. Lateral Phalanx	3	0.125	37.5	8	0.046
M. Lateral. Phalanx	0	0	0	8	0.046
D. Lateral Phalanx	4	0.167	50.0	8	0.046
Vertebra	2	0.083	4.7	42	0.241
TOTAL	25			174	

Table 9. Values of r_S for Spearman rank-coefficient test (Sokal and Rolf 1981). Number of ranks in sample indicated by n.

A. Comparison of skeletal-part frequency ranks of Thomas Farm bone assemblages from different sedimentary levels to one another and to a complete skeleton.

	Sedimentary Units						
	5	6	7	8	6-8	11	15
n	16	16	16	16	16	16	16
Complete Skeleton	**.878	**.829	**.915	**.756	**.900	**.787	**.776
Unit 5		**.807	**.946	**.779	-	**.864	**.680
Unit 6			**.879	**.898	-	**.849	*.607
Unit 7				**.851	-	**.926	*.629
Unit 8					-	**.830	*.537
Unit 11							*.488

B. Skeletal-part frequency ranks of Thomas Farm bone assemblages and a complete skeleton compared to Recent bone assemblages. (a) wolf kill site (Binford 1981 Table 5.01, col. 25); (b) wolf den (Binford 1981, Table 5.01, col. 27); (c) surface assemblage (Behrensmeyer and Boaz 1980, Table 5.6); (d) hyaena den (Behrensmeyer and Boaz 1980, Table 5.6).

	(a)	(b)	(c)	(d)
n	10	10	8	8
Complete Skeleton	.491	.406	*.780	.434
Unit 5	.558	*.760	.428	.381
Units 6-8	.433	.545	.404	.333
Unit 11	*.645	*.685	.571	.667
Unit 15	.118	.254	.470	.339

C. Relative representation values of Thomas Farm bone assemblages compared to (a) wolf kill site (Binford 1981, Table 5.01 , col. 26); (b) wolf den (Binford 1981, Table 5.01, col. 28), and (c) topi bone assemblage (Hill's data, from Binford 1981, Table 5.02, col. 2).

	(a)	(b)	(c)
n	10	10	10
Unit 5	.257	.330	.217
Units 6-8	.090	.078	-.213
Unit 11	.527	.527	.062
Unit 15	.106	-.021	-.250

**significant at 0.01 level
*significant at 0.05 level

demonstrated in Figure 22A. Placement of each element type from left to right along the X axis of this graph (and subsequent graphs, Figs. 22B-D, 23, and 24) corresponds to its equivalent quartz grain diameter, from largest to smallest, and therefore to the element's predicted tranportability in moving water.

The unit 5 bone assemblage is characterized by higher proportions of lateral metapodials and proximal and medial phalanges, and lower representations of vertebrae and distal phalanges than those of a complete skeleton (Fig. 22A). Relative representation values are based on dentaries (Table 8 and Fig. 23A) and with the exception of the astragalus and calcaneum, it is the lightest, smallest elements such as vertebrae, patellae, and distal phalanges that show the lowest representation. Statistical comparison of unit 5 skeletal-part frequencies with those of a complete skeleton using the Spearman rank-coefficient test, which provides a pairwise comparision of abundance ranks (Sokal and Rolf 1980), shows that the pattern of abundance is highly correlated with that found in a living animal (Table 9). Unit 5 skeletal-part frequencies show no significant correlations with kill sites (Binford 1981:Table 5.01, col. 25; Table 5.02, col. 2) or with an attritional assemblage (Behrensmeyer and Boaz 1980; Table 9). The Recent bone assemblages are similar to one another, and somewhat different from the unit 5 assemblage (Fig. 24), in the high relative representations of skulls, pelvic girdle elements, and vertebrae and low relative abundances of podials and phalanges (Binford 1981; Behrensmeyer and Boaz 1980). Blumenschine (1986) reported that some large carnivores may selectively remove or chew on distal appendages, thereby destroying podials and phalanges. Behrensmeyer and Boaz (1980) also attributed low representations of these elements in the surface assemblage to the actions of carnivores and scavengers, but noted that trampling can cause rapid burial of podials and other small bones. The fairly high representations of these bones in unit 5 suggests that the assemblage does not represent a surface accumulation formed or modified by carnivores and scavengers.

Comparison of skeletal-part frequencies in unit 5 with those of carnivore den assemblages (Binford 1981; Behrensmeyer and Boaz 1980) shows a correlation in frequency rank between the fossil assemblage and the den assemblage formed by wolves (Binford 1981: Table 5.01, col. 27). The assemblages are similar in the higher-than-expected proportions of limbs and podials and the low abundances of vertebrae (Fig. 22A, 24C). In terms of relative representations, the patterns of abundance appear similar (Fig. 23A, Fig. 24D), although the correlation between the two assemblages is not significant (Table 9C).

Moderate to high relative representation of all but the lightest elements in the unit 5 fossil assemblage suggests that the bones were not transported as a group by moving water. The presence of elements having a wide range of quartz grain equivalent diameters from extremely large to small would require

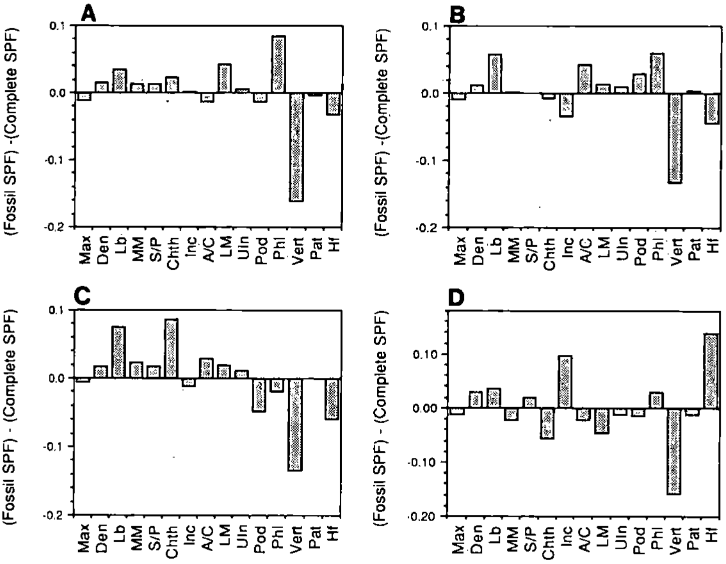

Figure 22. Graphic depiction of differences between skeletal-part frequencies of *Parahippus leonensis* remains from Thomas Farm and skeletal-part frequencies of a complete *P. leonensis* skeleton [(Fossil SPF) - (Complete SPF)]. (A) Unit 5. (B) Units 6-8 combined. (C) Unit 11. (D) Unit 15. Abbreviations: A/C, astragalus and calcaneum; Chth, cheekteeth; Den, dentary; Hf, distal phalanx (hoof); Inc, incisor; Lb, limbs (humerus, radius, femur, tibia); LM, lateral metapodials; Max, maxilla; MM, medial metapodials; Pat, patella; Phl, proximal and medial phalanges; Pod, podials except astragalus and calcaneum; S/P, scapula and pelvis; Uln, proximal ulna; Vert, vertebrae.

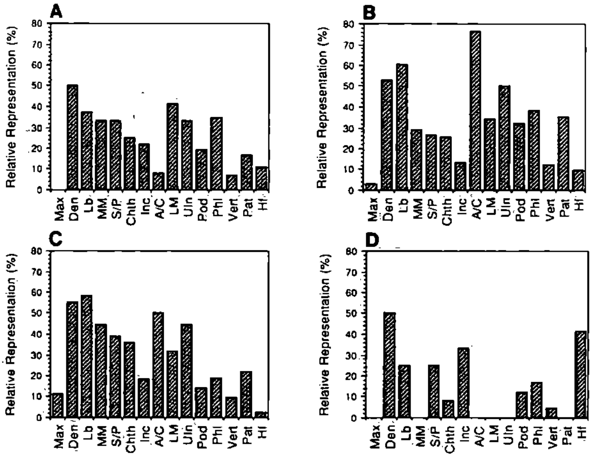

Figure 23. Relative representations of skeletal elements of *Parahippus leonensis*. (A) Unit 5. (B) Units 6-8 combined. (C) Unit 11. (D) Unit 15. See Figure 22 for list of abbreviations.

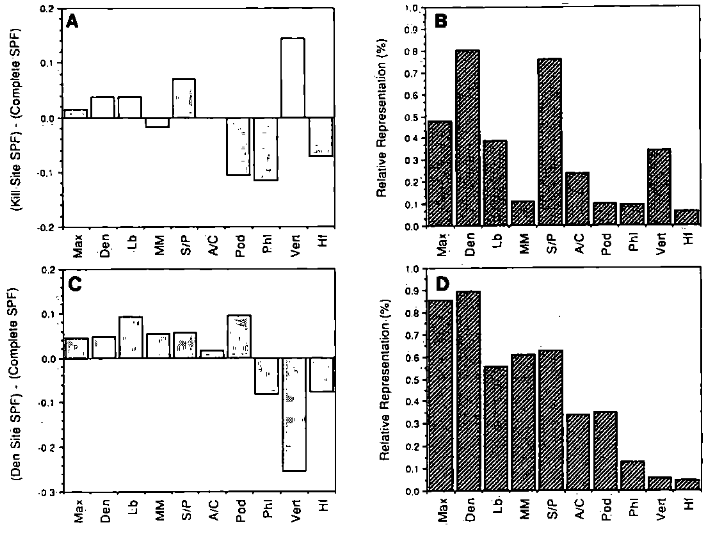

Figure 24. (A and C) Differences between skeletal-part frequencies of bones abandoned by wolves at a kill site (A), or brought to a wolf den site (C) and skeletal part frequencies of a complete artiodactyl skeleton. (B and D) Relative representations of bones abandoned by wolves at a kill site (B), or brought to a wolf den (D). All data from Binford (1981). See Figure 22 for list of abbreviations.

that the agent of transport be a stream of high competence, capable of carrying the entire assemblage from elsewhere. The lack of sedimentological evidence indicating fluvial transport and the absence of water-wear on elements belonging to transport groups III and II suggest that the majority of the elements were not brought into the sinkhole in this fashion. However, the low representations of the lightest elements do indicate that the bone assemblage in the sink was modified by the action of moving water, and the lightest elements may have been removed by winnowing. Figure 23A shows that transport groups III and II elements possess the highest mean relative representation values, followed by group I/II elements, and finally group I elements. This pattern is similar to the 1B model of Hanson (1980, Fig. 9.3).

Units 6-8. Units 6, 7, and 8 are similar not only in lithology but in faunal content and skeletal representation as well (Tables 4, 8). It has been suggested in previous sections that the bone assemblages in these units were formed under very similar circumstances. For these reasons, the bone counts from units 6 through 8 were combined to form a large sample (Table 8). The calculated MNI decreases from 21, if the MNI for each layer are summed, to

17 if the 3 layers are treated as one. However, lumping the sample from these three sedimentary units does not affect the order of representation of elements from most to least abundant.

Skeletal-part frequency ranks of combined units 6-8 elements are highly correlated with those of a complete skeleton (Table 9A, Fig. 22B). The bone assemblage is similar to that of unit 5 and unlike Recent kill site accumulations modified by carnivores (Table 9, Fig. 24A) in higher-than-expected frequencies of podials and phalanges, and lower-than-expected frequencies of vertebrae. Bone frequencies also are not highly correlated with those of carnivore den sites (Table 9B, Fig. 24). Units 6-8 differ from the lower sedimentary level in the higher representations of elements, such as astragali, that are classified as transport group I/II elements (Fig. 23B). The apparent enrichment of these elements in the accumulation may be attributed to transport by moving water. It is possible that water moving through underground drainage networks transported these lighter elements from another more distant bone source, perhaps another sinkhole, and added to them to the assemblage within the Thomas Farm sinkhole. This interpretation is supported by the observation that the majority of abraded, water-worn bones within units 6, 7, and 8 are those possessing quartz grain equivalent diameters of 6 mm or less. Slowing of current velocity within the sinkhole would cause deposition of all but the lightest group I elements, which were then carried out of the sink by the somewhat reduced current.

Unit 11. The assemblage of *Parahippus leonensis* elements in unit 11 is the most problematical, because not only do skeletal-part frequency ranks resemble those in a complete skeleton, they are also similar to bone abundances of a carnivore kill site and a den site (Table 9A & B, Figs. 22C, 24). In terms of relative representations of elements, no significant correlations with either type of carnivore-modified accumulation are indicated (Table 9C). The pattern of relative representation values more closely resembles that of a carnivore den site, in which the largest densest elements, such as dentaries and limbs, are represented in higher abundances than smaller and less dense elements (Figs. 23C, 24D). This pattern also resembles the type 2A model of Hanson (1980, Fig. 9.3) of a lag deposit; however, there is less evidence of aquatic influence in unit 11 than in the lower clay and sand layers. The fact that the layer is composed of large limestone boulders might lead to the assumption that the remains were initially deposited in a cave by scavengers, and fell into the site as the cave walls and floor collapsed. However, the lack of bone showing any evidence of destruction by gnawing suggests that this interpretation is not the most acceptable. The small sample size of cranial material from unit 11 does not allow testing of the hypothesis that the horses were killed in a catastrophic event as the wall fell (Hulbert pers. comm.), but the presence of bones throughout all levels of the boulder layer suggests that neither the boulders nor the bones were deposited instantaneously. The composition of the sediment itself may have been the dominant factor in determining the composition of the bone assemblage. Losses of the lighter, less dense elements may have been due to crushing and compaction of these bones by large boulders as the layer was deposited, as well as by subsequent post-depositional compaction.

Unit 15. The number of equid specimens in unit 15 ($n = 63$) is too low to allow for statistical analysis of skeletal percentage preservation. Megafaunal remains within unit 15 are dominated by incisors, phalanges, podials, and vertebrae (Fig. 22D, 23D). Limb bones, with the exception of small fragments or epiphyses, are rare. Based on high abundances of microfaunal elements, it is probable that remains in this layer represent a coprocoenosis formed by small canids (Pratt 1986, 1989).

Skeletal-Part Preservation: Summary

Although skeletal-part compositions of the bone accumulations in several sedimentary layers do show correlations with either carnivore kill sites or dens, bone abundances in the various layers are most similar to one another and to bone abundances in a complete skeleton (Table 9). Therefore, it is logical to conclude that the original death assemblages were relatively unmodified by weathering, scavenging, or transport. If the site acted as a trap, the above conclusion would imply that the carcasses were rapidly made innaccesible to modification by these agents. However, the lack of skeletal articulation indicates that sufficient time must have elapsed prior to burial to allow for complete disarticulation. Agenbroad (1984) suggested that disarticulated mammoth remains in Hot Springs, South Dakota, were deposited from rocky talus slopes near the base of the sink, or from carcasses floating in the water of the spring. It has been shown that carcasses submerged in water may float, and as ligaments and tendons decompose, bones fall to the bottom of the water body (Dodson 1973; Hill 1980). This scenario is a plausible one for explaining the source of many of the Thomas Farm elements. The similarity of several of the Thomas Farm bone assemblages (unit 7 and 11) to carnivore den deposits is more likely due to the fact that several very different types of taphonomic agents all may cause loss or destruction of the lightest, smallest elements (Hanson 1980; Behrensmeyer 1982; Andrews and Nesbit Evans 1983). The lack of gnawed or chewed bone suggests that moving water, rather than carnivores, was responsible for the removal of group I elements. This conclusion is consistent with previous observations that have suggested the presence of an underground water source associated with the sink. The hypothesis that moving water played a role in formation of the Thomas Farm assemblage can be further tested by consideration of bone orientations, discussed in the following section.

Bone Orientation

Recent experimental work has shown that moving water is not only capable of transporting skeletal elements, but also of influencing their orientations within the sediment (Voorhies 1969; Saunders 1977; Hunt 1978; Shipman 1981, Maas 1985). Direction of flow and, to some degree, current velocity may be inferred by recording directional and positional orientations of bones in a fossil assemblage. Orientations of the long axes of limb bones are the most reliable indicators of current direction (Voorhies 1969). The degree of dip of a bone within a sedimentary layer measured along the element's long axis (plunge) may also be related to paleocurrent strength (Voorhies 1969). The shape of a bone influences its preferred orientation or stable resting position in the presence of moving water. A fluvial system with a current velocity sufficient to cause movement or transport of long bones (required velocities vary depending on the size of the bones and physical characteristics of the stream) is recognized by a rose diagram similar to that illustrated in Figure 25A (Voorhies 1969; Shipman 1981). Long bones are positioned with their long axes parallel to the prevailing current direction and their less dense articular ends facing downstream (Voorhies 1969). Shorter bones, or cylindrical elements with ends of more or less uniform density, tend to align perpendicular to the current. Figure 25B shows a proposed orientation pattern caused by sheetwash down an incline. Bones are oriented with the long axes parallel to maximum dip of the slope, and on either side of maximum dip. In Figure 25C, a uniform or non-preferred orientation pattern is illustrated, which in most circumstances indicates absence of a strong, unidirectional current. A uniform orientation pattern also may be produced by multidirectional flow such as that produced by an artesian spring (Saunders 1977), or by flow that periodically changes direction. It should be remembered that the rose diagrams pictured in Figure 25 represent orientations of hypothetical bone assemblages, and variation from these patterns does not necessarily signify the absence of water-related orientation. Rose diagrams based on actual data are usually more complex than predictive models, so all aspects of bone position, not just bearing, should be considered in analysis of a fossil bone assemblage. Nevertheless, if bone orientation has been influenced by a non-random directional factor, then the distribution of bone orientation direction tends to be significantly different from a distribution in which no preferred orientation pattern is evident (Shipman 1981). The presence of a non-uniform orientation pattern can be determined by use of the Chi-square goodness of fit test (Sokal and Rohlf 1981). Bone orientations are considered significantly different from non-preferred or uniform at the $p = 0.01$ level.

Thomas Farm Bone Orientations

Entire Site. The rose diagram showing orientations of bones collected from all fossiliferous levels of the site (Fig. 26A) does not resemble that of a fluvial environment (Fig. 25A). The pattern of bone orientations (arranged in 10° increments) is not significantly different from that expected if the bones were distributed uniformly (Table 10); however, there are significantly more bones aligned toward the northeast/southwest quadrants (62%) as opposed to the southeast/southwest quadrants (Table 10).

By considering bone plunge as well as bearing, a stereonet may be constructed in which each bone is indicated by a point whose coordinates are bearing direction and degree of plunge (Voorhies 1969; Shipman 1981). Figure 26B shows the stereonet of bearings and plunges for all elements on which these readings were taken (n = 516). The predominance of points in the southwest quadrant does not reflect the actual bone plunge direction, but the dip of the sediments, which tend to obscure the plunge of the bone relative to the bed. In order to determine the true plunge of the bone relative to the sediment layer, its degree of plunge must be corrected for the dip of the bed in which it is found (Shipman 1981:78). Once this step is accomplished, a stereonet constructed using the corrected values shows that a number of bones actually plunge northeast within the sediments (Fig. 26C). This pattern is unlike that seen in a fluvial deposit (Voorhies 1969). Voorhies suggested that in a fluvial environment the majority of bones behave like boulders by imbricating and dipping upstream. In this case, the majority of bones should be dipping in one direction. No such trend is evident in the corrected stereonet. Significantly greater numbers of bones plunge either northeast or southwest as opposed to northwest or southeast, but there is no significant difference in the numbers of bones plunging northeast as opposed to southwest (Table 10). Degrees of plunge are shallow, and in most cases do no exceed 15°.

Elimination from the rose diagram and stereonet of elements shown experimentally (Voorhies 1969; Korth 1979; Pratt 1979) to have preferred orientations in directions other than parallel to the prevailing current (scapulae, carpals, phalanges, pelves, patellae, tarsals, vertebrae) results in the rose diagram and corrected stereonet shown respectively in Figures 27A and B (n = 337). The significant northeast/southwest trend of the rose diagram is evident, with over 70% of the elements' long axes aligned with this compass direction, as opposed to 30% aligned to the southeast/northwest (Table 10). However, the orientation pattern (in 10° increments) is not significantly different from a uniform, non-preferred orientation distribution (Table 10). The stereonet of long bone bearings and plunges corrected for the dip of the

Table 10. Chi-square values for compass orientations of skeletal elements. Orientation patterns considered significantly different from a uniform pattern if $P \leq 0.01$. Abbreviations: D.F., degrees of freedom; Met., metapodials; N, number in sample; *P*, probability value; Prox., proximal.

CATEGORY	N	D.F.	X^2	*P*
All Elements/Entire Site	913	17	9.24	0.900
All Elements (by quadrant)	913	3	53.06	<0.005
Long Bones/Entire Site	337	17	8.70	0.950
Long Bones (by quadrant)	337	3	54.04	<0.005
Direction of Plunge (NE vs. SW)	187	1	1.18	0.600
All Elements/Unit 5	99	17	33.76	0.010
Long Bones/Unit 6	71	17	59.57	<0.005
Long Bones/Unit 7	60	17	76.63	<0.005
Long Bones/Unit 8	72	17	45.70	<0.005
Long Bones/Unit 11	96	17	32.40	0.125
Humeri/Entire Site	46	17	40.83	<0.005
Tibiae/Entire Site	62	17	87.38	<0.005
Medial Met./Entire Site	86	17	34.31	0.010
Lateral Met./Entire Site	84	17	33.07	0.125
Prox. Phalanges/Entire Site	69	17	34.11	0.010

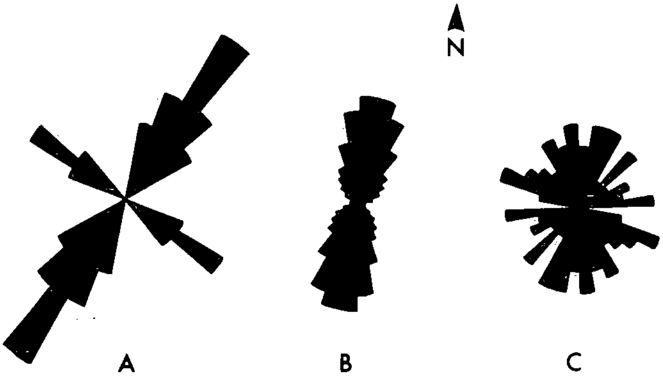

Figure 25. Hypothetical bone orientation patterns. (A) Fluvial system with prevalent current direction NE/SW. (B) Sheetwash down an incline showing bone orientations following maximum SW slope of beds. (C) Uniform or non-preferred orientation pattern (from Shipman 1981).

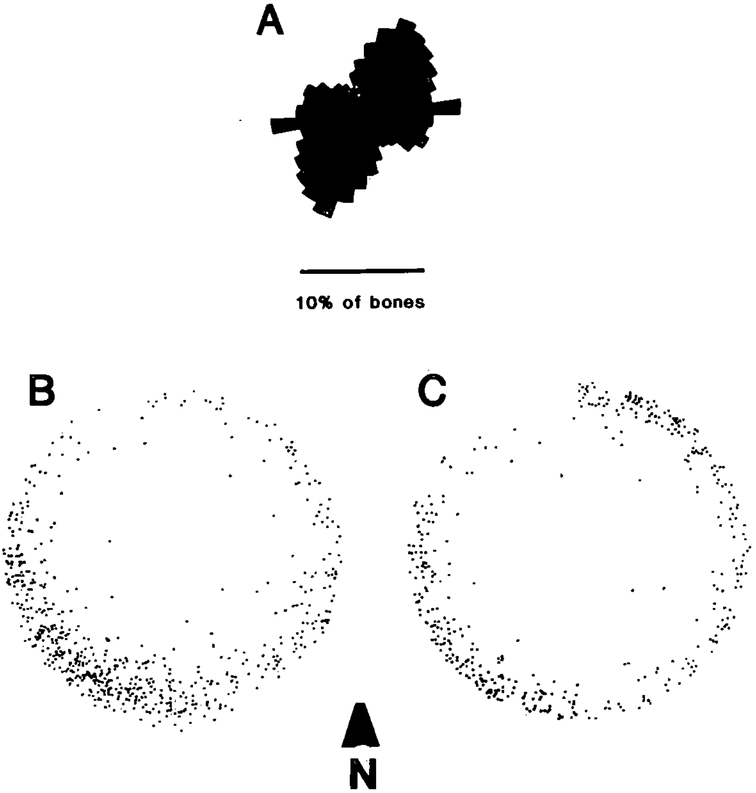

Figure 26. Orientation patterns of megafaunal elements at Thomas Farm. (A) Rose diagram showing orientations of all bones measured at Thomas Farm. (B) Stereonet, not corrected for dip of beds, showing bearings and plunges of all bones measured. (C) Stereonet, corrected for dip of beds, showing corrected bearings and plunges of all bones measured.

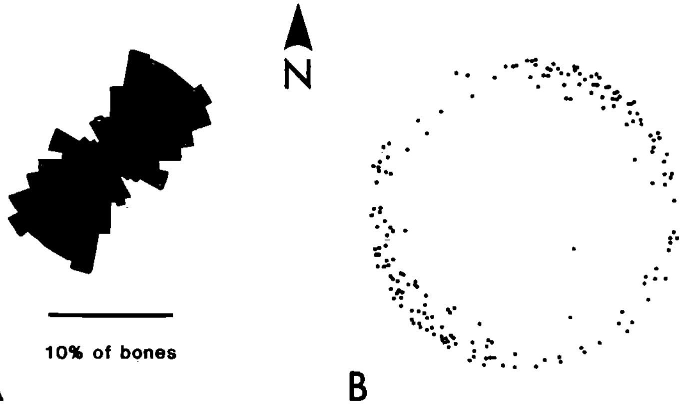

Figure 27. Orientation patterns of long bones. (A) Rose diagram showing orientations of all long bones measured. (B) Stereonet, corrected for dip of beds, showing bearing and plunges of all long bones measured.

beds shows that the majority of the bones plunge northeast or southwest, but there is no significant difference in the numbers of bones plunging northeast as opposed to southwest (Table 10). The high uniformity in direction and degree of bone plunge and the relatively low angles of plunge indicate that it is unlikely that bones were trampled into the soft sediment. Bones trampled in soft sediment reportedly exhibit high degrees of plunge (Andrews et al. 1981).

Treating the Thomas Farm site as a single homogeneous deposit results in the misleading conclusion that the bones do not show a significant orientation pattern, although the majority of limb elements do show bearing directions to the northeast/southwest. If each major sedimentary unit is considered separately, more definite orientation patterns emerge.

Unit 5. Fossils on which it was possible to obtain orientation measurements were not very numerous in unit 5 ($n = 99$). The rose diagram of all bone bearings in unit 5 shows a northeast/southwest trend in orientations. The greatest numbers of bones are aligned from from 40-70/220-250 degrees east of North, with over 30% of the bones located within this 30° span. The distribution of bone directions in Unit 5 is significantly different from uniform (Table 10). The sample size of limb bones (long bones) from unit 5 is too small to test statistically for evidence of preferred bearing direction ($n = 22$). Over 25% of the elements are oriented with their long axes pointing 70/260 degrees east of North (Fig. 28A), suggesting that some factor was causing alignment of the long bones toward this direction.

Unit 6. Long bones collected from unit 6 display a significant pronounced orientation trend (Fig. 28B, Table 9). Most of these elements are oriented from 10-40/190-220 degrees east of North, with a smaller peak at approximately 90° to the major orientation peak. The bimodal shape of the rose diagram bears some similarity to that of a fluvial or current-influenced assemblage.

Unit 7. Unit 7 bone orientations are similar to those of unit 6, although the spread of preferred direction is wider. The orientation pattern of long bones only (Fig. 28C) is significantly different from that of a uniform array (Table 10). Based on the similarity of the rose diagrams for units 6 and 7, it is evident that factors responsible for bone alignment did not change dramatically during the time period in which these two layers were deposited.

Unit 8. In unit 8, skeletal element orientations are not as clearly defined as in the lower two layers, 6 and 7. The more diffuse pattern seen in Figure 28D is probably related to the fact that unit 8 is not uniform sedimentologically. The distributions of long bones ($n = 72$: Fig. 28D) do show a statistically significant orientation pattern (Table 10). Although the

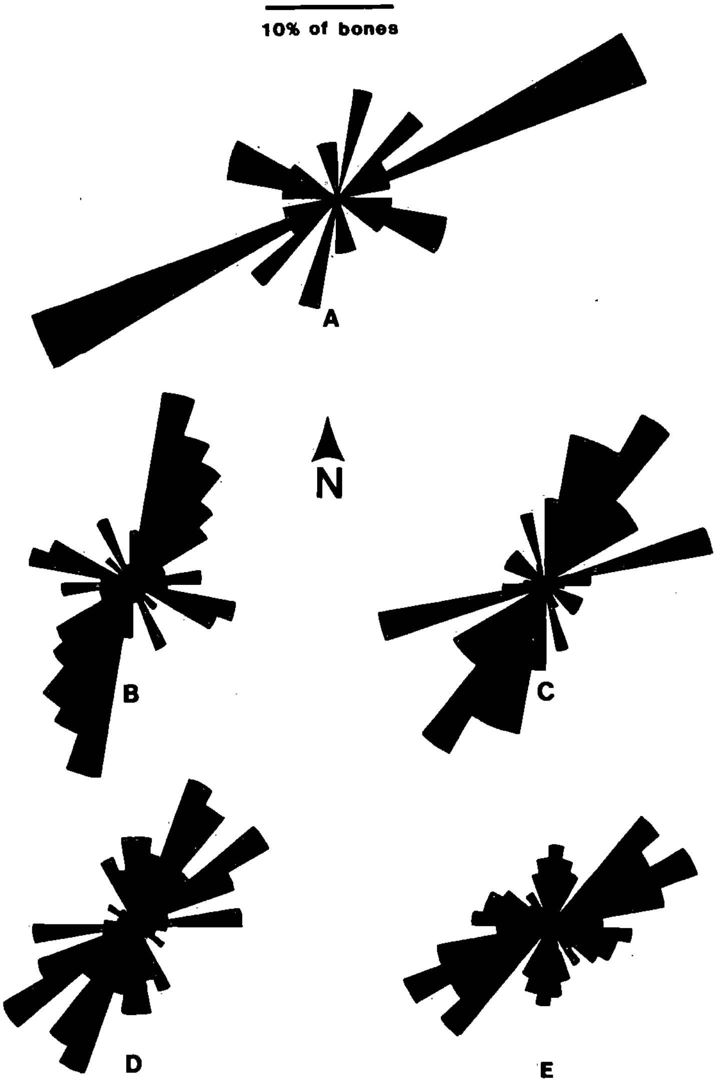

Figure 28. Rose diagrams of bearings of long bones collected from major sedimentary units. (A) Unit 5. (B) Unit 6. (C) Unit 7. (D) Unit 8. (E) Unit 11.

preferred bone direction is not as obvious as in units 6 or 7, the majority of long bones (73%) are oriented to the northeast/southwest.

Units 11 and 15. If long bones only (n = 96) from unit 11 are plotted, (Fig. 28E) the dominant preferred orientation is between 40-80/220-260 degrees east of North. However, the orientation pattern is not significantly different from uniform at the 0.01 level (Table 10). No rose diagrams have been plotted for unit 15, as the number of bones collected with complete orientation data was very low (n = 8).

The presence of preferred bone orientations to the northeast/southwest clearly shows that some agent, perhaps moving water, was responsible for bone alignment. If a current is to be implicated as a major cause of bone alignment, it is necessary to determine if evidence of unidirectional flow, either from northeast to southwest, or from southwest to northeast, can be determined. The compass bearing of a skeletal element provides only a portion of the information that can be obtained concerning possible current direction and environment of deposition. To accurately determine the speed and direction of paleocurrent flow, a bone's specific behavior as a paleocurrent indicator must be examined. This procedure requires experimental analysis using modern bones as means of documenting the hydraulic behavior of skeletal elements in a variety of aquatic situations.

Orientation and Positions of Selected Element Types

Skeletal elements may be separated into groups according to their usefulness as paleocurrent indicators. Based on data from previous flume studies (Voorhies 1969; Pratt 1979), and recently conducted fluvial experiments using skeletal elements of Recent deer, which are similar in general size and shape to *Parahippus leonensis* elements, I have classified skeletal elements according to their usefulness as paleocurrent indicators:

> Category A: Bones that show a preferred axis of orientation, and usually possess one end that repeatedly orients downcurrent. Elongate limb elements are included in this group and are of most use in determining direction of prevailing current.
>
> Category B: Elements that do not necessarily indicate prevailing current direction, but may exhibit predictable stable orientations or resting positions in running water. Included in this group are the pelvis, astragalus, calcaneum, and proximal phalanges, and alligator osteoderms. Positions of these bones may provide evidence that deposition occurred under conditions of moving water, as opposed to standing

water, and indicate, in a general way, strength of current, as a bone may assume a stable resting position at current velocity just below critical transport velocities for the bone.

Category C: Bones that do not show any preferred orientations. Most of the elements in this group are small in size and are not elongated in any one dimension. Carpals, tarsals, and distal phalanges have limited usefulness as paleocurrent indicators, and are included in this category. For obvious reasons, category C will not be discussed in the following analysis.

In the following discussion, each sedimentary unit will not be described individually, as numbers of each bone type from any one level are too small to allow for statistical analysis. The overall similarity of bone orientation direction throughout all units studied justifies lumping the samples from these layers to obtain a large, statistically significant sample.

Orientation Behavior of Category A Elements. Most long bones, particularly limb elements, tend to orient with their long axes parallel to the direction of running water (Voorhies 1969; Hanson 1980). Some bones may also orient at right angles to the current. Field positions and orientations of fossil bones are compared with orientations observed for Recent bones in controlled and natural fluvial environments (Voorhies 1969; Boaz and Behrensmeyer 1976; Pratt 1979, 1986). Voorhies (1969) observed as a general rule that the larger end of a long bone tends to orient in the downstream direction. Pratt (1979), showed that it is not necessarily the larger end that points downcurrent, but the less dense (frequently air-filled) end that is moved into the downstream position. This finding is particularly true of long bones that have been exposed to the drying effects of weathering.

Humerus. Long axes of fossil humeri from Thomas Farm (n = 46) clearly align with the predominant preferred direction (Figure 29A). The majority of these elements are found lying between 40-80/220-260 degrees east of North. The directional distribution of humeri is significantly non-uniform (Table 10). The directions that the ends of the humeri point may be assessed by examining complete fossil humeri. Of thirteen whole humeri, 2 were found with the proximal end pointing northeast, 5 with the proximal southeast, 5 with proximal southwest, and 1 with proximal northwest (Table 11). Voorhies' flume experiments (1969) showed that the "larger" (interpreted here as proximal) ends of humeri of sheep, coyotes, and badgers oriented downstream in about 85% of the runs. In flume experiments on rabbit to raccoon-sized skeletal elements (Pratt 1979), proximal ends of humeri oriented downstream about 65% of the time (37/56 trials). Experiments conducted in conjuction with this study showed that fresh and weathered deer humeri placed in a small stream were transported, and came to rest, with the proximal ends facing downstream in 5 of 5 trials. Humeri of Recent deer dropped from a horizontal position into standing water fell with the denser distal end first (provided both epiphyses were present). If the proximal end was air-filled, as was observed in several trials, the humerus floated in a vertical position with the proximal end floating at the surface. The lighter proximal end often leads the way as the element is transported downstream.

Distal portions of humeri are the most abundant parts of this element found at the Thomas Farm. Little experimental work has been conducted on orientation patterns of broken skeletal remains, although Boaz and Behrensmeyer (1976) recorded the final orientation of a hominid distal humerus in a flume as distal downstream. Of the 25 distal humeri in the fossil deposit, 14 (56%) are oriented with the distal end pointing to the southwest, indicating that distal humeri exhibit a preferred orientation, probably in the downcurrent direction. More experimental work is needed to confirm the correctness of this statement.

The positions in which the humeri are found in the field also indicate that certain orientations are more stable than others. Complete humeri are most often found medial or posterior side up, while distal portions only are most frequently found posterior side up.

Radius. The orientations of 35 fossil radii are shown in the rose diagram in Figure 29B. Although this element is too poorly preserved at Thomas Farm to be of use in statistical determination of a preferred current direction, almost 80% (28) of the radii point either northeast or southwest, documenting the bone's tendency to be aligned parallel to the prevailing current direction.

The differences in size and density of the two ends of the radius are not as pronounced as are those of the humerus, however, 5 of 8 (63%) complete radii were found with the distal end pointing southwest (Table 11). Voorhies (1969) found that the larger ends (he did not specify the end, it is assumed that he was referring to the distal end) of sheep and coyote radii oriented downstream 72% of the time. Flume experiments on radii of small mammals (Pratt 1979), showed no significant preferred end orientation for this element. Recent deer radii dropped from a horizontal position into standing water fell with the proximal end first, but the distal end did not float.

Broken proximal and distal ends of fossil radii do not show a clear pattern of end orientation, and no conclusions can be drawn from these data. The majority of radii were found either with the anterior or posterior surface up. This position is to be expected, particularly for *Parahippus* radii, which are flattened in the anterior-posterior plane.

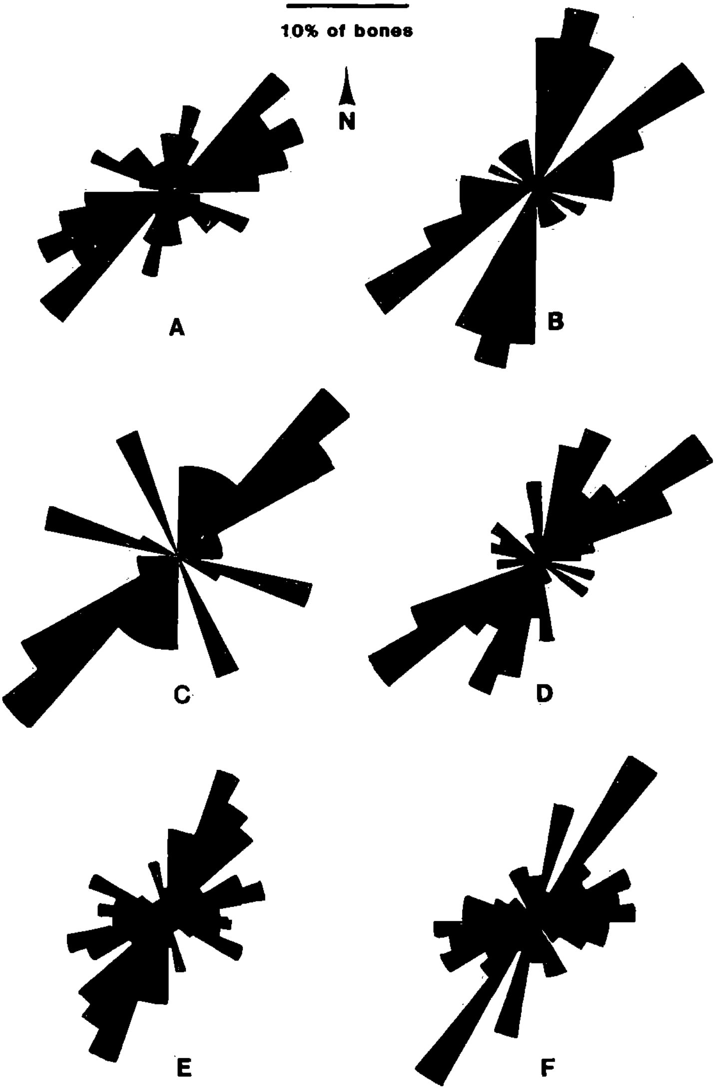

Figure 29. Rose diagrams of bearings of selected "category A" long bones. (A) Humerus. (B) Radius. (C) Femur. (D) Tibia. (E) Medial metapodial. (F) Lateral metapodial.

Table 11. Positional orientations of Thomas Farm elements. Data are for complete elements only. Shown are proportions of elements with predicted downstream end pointing to each compass quadrant. For discussion of downstream indicators and abbreviations, see text.

Element	n	Predicted downstream end	% with predicted downstream end			
			NE	SE	SW	NW
Humerus	13	proximal	15.4	38.5	38.5	7.6
Radius	8	distal	12.5	12.5	62.5	12.5
Femur	12	distal	16.7	8.3	50.0	25.0
Tibia	26	proximal	7.7	7.7	76.9	7.7
Medial metapodial	35	distal	28.5	14.3	42.9	14.3

Femur. Few femora were collected on which orientation data could be taken (n = 27), and it is not possible to conduct a Chi-square test to determine if their pattern of orientation, shown in Figure 29C, is significantly different from that expected in a uniform distribution. Roughly 33% of the femora are aligned within the 40-60/220-240 degree range of bearings.

Of 11 whole femora, 6 were found in the field with the distal end facing southwest, 2 with the distal northeast, 1 with the distal end southeast, and 3 with the distal northwest (Table 11). Voorhies (1969) showed that the larger (it is assumed he meant distal) end of the femur oriented downstream in 78% of the flume runs. Femora of smaller mammals were also found aligned with the distal end facing downcurrent in 72% of the runs (Pratt 1979). Recent deer femora usually possess distal ends that are lighter than the proximal ends, and although both ends may initially float, the proximal end invariably becomes waterlogged first. In one experiment, a deer femur was placed in water. The proximal end sank immediately, but the distal end remained floating for five hours. In a natural fluvial environment, a weathered femur was transported, bobbing along the water surface for a distance of over 150 m, until the distal end became waterlogged. In all trials conducted, the distal end faced downstream when the bone ceased movement.

Fossil proximal and distal femur portions are not abundant enough to indicate clearcut trends in orientation, although the majority of incomplete elements were recovered with the broken end pointing toward the southwest. Experiments in the laboratory on distal femora showed that the broken end oriented downcurrent in 66% of the trials. The preferred resting orientation of a complete femur is posterior surface up. A total of 6 complete femora were found in this position, and 3 were found anterior surface up.

Tibia. The orientation of fossil tibiae from the Thomas Farm (n = 62) is significantly different from uniform at the P= 0.001 level (Table 10). The rose diagram of tibia orientations (Figure 29D) shows the preferred axis of orientation at 40-70/220-250 degrees east of North, similar to that of the other limb bones discussed above. Voorhies (1969) noted that the orientation of the mammalian tibia was a reliable indicator of paleocurrent direction, as this element most often comes to rest with the long axis parallel to the current and the large proximal end facing downstream. In Voorhies' flume experiments, the tibia was found in this position in over 90% of the trials. Flume studies on small mammal bones (Pratt 1979) showed that the tibia oriented with the proximal end downstream 87% of the time. Recent deer tibiae placed in a small stream resisted movement in most cases, and in other trials rolled perpendicularly to the current. An orientation of a long bone at right angles to the current most often results when the water depth is not sufficient to totally immerse the bone (Voorhies 1969). The proximal end of the tibia, in addition to being a good deal larger than the distal end in size, may also frequently be air-filled in a naturally dried skeleton, as evidenced by studies on deer tibiae. Tibiae of adult deer, if dropped from a horizontal position, always fell through standing water distal end first. Weathered bones sometimes initially floated vertically with the distal end down.

The tendency for the fossil tibiae from Thomas Farm to orient with the proximal end pointing predominantly in one direction is clearly seen. Of 26 complete tibiae, 20 (over 77%) were recovered with the proximal end pointing southwest, providing strong evidence that water moved through the deposit from the northeast towards the southwest (Table 11). No definite orientation trend is evident for the broken proximal or distal ends of the tibia.

The preferred resting orientation of the whole tibia is medial side up. Over 38% of the tibiae (10 of 26) were found in this position at Thomas Farm. The bone may also come to rest with the posterior, but rarely the antero-lateral surface, facing upward.

Metapodial. Relatively little experimental work has been done concerning the behavior of metapodials in hydrodynamic conditions. Fossil metapodials will be discussed as two groups, the "medial" metapodials, such as metacarpal III and metatarsal III of horses and metacarpal and metatarsal III/IV of artiodactyls, and the "lateral" metapodials of three-toed horses. Metapodials of carnivores are not included, as orientation data were taken on relatively few of these elements. Medial metapodial orientations (n = 84) are shown in Figure 29E. Over 30% of these bones are aligned in a 20-50/200-230 degree wedge on the rose diagram. The orientation pattern is significantly different from that expected in a uniform distribution (Table 10). Recent deer metapodials dropped from a horizontal position into standing water showed no preferred settling orientation, presumably because both ends are similar in size and density. It is therefore not expected that this element would exhibit a preferred end orientation. Deer metapodials in a stream may roll perpendicularly to the current or be moved parallel to it. When placed in running water, these elements came to rest with the distal end facing downstream in 66% (3 of 5) of the trials. Of 35 complete medial metapodials from the Thomas Farm, 15 (43%) are oriented with the proximal end pointing southwest and 10 (28%) with the proximal end pointing the opposite direction. The remaining 10 are equally divided; 5 with proximal ends facing northwest and 5 with proximal southeast (Table 11). The lack of difference in density between the two ends of a metapodial limits the usefulness of this bone as an indicator of direction of prevailing current.

If distal portions of medial metapodials only are considered, 45% (14 of 31) point distal southwest, as opposed to 25% (8) pointing northeast, 19% (6) northwest, and 11% (3) southeast. Proximal fragments are most often found with the proximal end facing downslope; of 15 proximal ends, 53% (8) are directed proximal southwest, and 33% (5) proximal southeast. Incomplete metapodials appear to be more useful in determining current direction than are complete metapodials.

The majority of medial metapodials are found lying either anterior or posterior up, although occasionally one may be found on its side. The nearly circular cross-section of a metapodial increases the likelihood that this bone will not show any preferred side-up resting position.

Lateral metapodials of three-toed horses are fairly well-represented at the Thomas Farm locality (n = 84). Most lateral metapodials have bearings between 30-40/210-220 degrees east of North (Figure 29F), although a large number of lateral metapodials are also found with their long axes lying between 60-90/260-270 degrees. The orientation pattern is not significantly different from uniform at the $P < 0.01$ level (Table 10). It is not possible to conduct comparative studies on these bones using Recent specimens, as these elements are absent in modern horses. Complete fossil lateral metapodials (n = 23) were recovered with proximal ends pointing equally to the northeast, southeast, and southwest. Only 2 were aligned with the proximal end pointing northwest.

No trend is seen for proximal ends of lateral metapodials, but 41% of distal fragments (9 of 22) were found with the distal end facing southwest. Lateral metapodials are almost always found lateral or medial surface up.

Orientation Behavior of Category B Elements. Although skeletal elements belonging to category B are not necessarily found with one axis consistently aligned in the direction of the prevailing current, these bones do exhibit some type of predictable orientation in the presence of running water.

Pelvis. Data were obtained on only 16 complete fossil pelves or pelvis fragments. Numbers of bearing readings taken on innominates are too few to show a directional trend, however, 13 of the 16 (81%) innominates mapped were found with the lateral (acetabular) surface up. In flume studies on large mammals (Voorhies 1969; Korth 1979) transport of complete pelves joined at the pubic symphysis has been observed. Complete pelves are usually rare at fossil localities, so these studies are of limited use in analysis of hydraulic behavior of fossil innominates. My studies on flume transport of innominates of small mammals (Pratt 1979) showed that innominates introduced into the flume with the medial surface up would eventually flip over and come to rest with the lateral surface up. Even under conditions of increased current velocity, these elements resisted further change in medial-lateral orientation. The majority of pelvic elements found at the Thomas Farm locality in the fluvially-stable position may indicate that current velocities were sufficent to cause these elements to be moved from a less stable position and come to rest with the medial surface down.

Astragalus and calcaneum. Ungulate astragali are cube-like in shape and do not show a dominant preferred directional orientation; however, 31% of the astragali found at the Thomas Farm were oriented with the proximal end facing southwest (14 of 44). The preferred resting orientation of the astragalus of *Parahippus* is with the trochlear or plantar surface up, as these sides are wider and flatter than the medial or lateral sides.

Of 44 calcanea, 14 (31%) were found with the proximal-distal axis oriented from 100-120/280-300 degrees east of North. The calcaneum evidently orients with its long axis perpendicular to the current direction, as well as parallel to it (Figure 30A). Studies on the behavior of the calcaneum in running water show that modern horse calcanea rotate about the distal ends, usually ending with the proximal articular ends pointing downstream, while deer calcanea most often point distal downstream. The fossil calcanea from the Thomas Farm were primarily equid calcanea and showed the former trend; 29 of the 44 specimens were found with the proximal end facing in the downslope direction. The majority of calcanea were found resting either on their medial or lateral sides, rather than on the narrow anterior or posterior surfaces. The tendency of the calcaneum to orient at right angles to, as well as parallel to the current direction limits its usefulness as a paleocurrent direction indicator, although the bimodal distribution of its orientations can serve to denote the presence of moving water.

Proximal phalanges. Proximal phalanges are common at the Thomas Farm locality. The digit elements found at the locality are primarily proximal phalanges of digit III of *Parahippus leonensis* and *Archaeohippus blackbergi*. Their orientation pattern, as shown on the rose diagram (Figure 30B), possesses two peaks, one parallel to the proposed current direction at about 30-50/210-230 degrees east of North, and a second, less well-defined peak at about 90-120/270-300 degrees, oblique to the first peak. Proximal phalanges can be classified as "rollers" (Hanson 1980), small, cynlindrical objects that orient either parallel or perpendicular to the current direction. The orientation pattern for proximal phalanges from Thomas Farm is significantly different from random at the $p = 0.01$ level (Table 10). The proximal end of a proximal phalanx of a modern deer is lighter than the distal end, and is swung into the downcurrent or downstream direction by moving water. In a stream, proximal phalanges of deer and horses are readily transported and always come to rest with the proximal end facing downstream. At the Thomas Farm, proximal phalanges are oriented primarily with the proximal ends oriented downslope (28 pointing proximal southwest, 24 pointing proximal southeast), suggesting their alignment reflects a paleocurrent gradient. Although orientations of phalanges are often ignored in taphonomic studies, these elements are sometimes abundant in fossil localities and can of some use as indicators of current direction.

Alligator osteoderms. Alligator osteoderms are rectangular or oval, so bearings are measured along the central keel. No preferred pattern of directional orientation is evident (Figure 30C). The notable feature of the fossil osteoderms is that over 75% (47 of 63) of the specimens were found with the external (keeled) surface up. Osteoderms of modern alligators dropped vertically through standing water most often land with the internal (non-keeled) surface up. In the presence of moving water, osteoderms resting on the keel are pulled over onto the flat internal surface. Once these bones have come to rest with the external surface up, they seem to resist further movement. The fact that most of, but not all, the fossil osteoderms are found in fluvially-stable positions indicate that an intermittent current such as that caused by the rapid draining of water through an opening in the bottom of a sinkhole, may have been responsible for rotating most of the osteoderms to a more stable resting position prior to their burial.

Bone Orientations: Summary

Long axis bearings of skeletal remains from all sedimentary units of Thomas Farm (except unit 15) clearly show an orientation trend to the northeast/southwest quadrants. The hypothesis that this pattern was produced primarily by moving water is supported by the positions of category A elements (Table 10), which without exception show a preferred "downstream" orientation toward the southwest. The predominance of category B elements showing fluvially stable resting positions or characteristic orientations are also indicative of influence by moving water. The proposed direction of

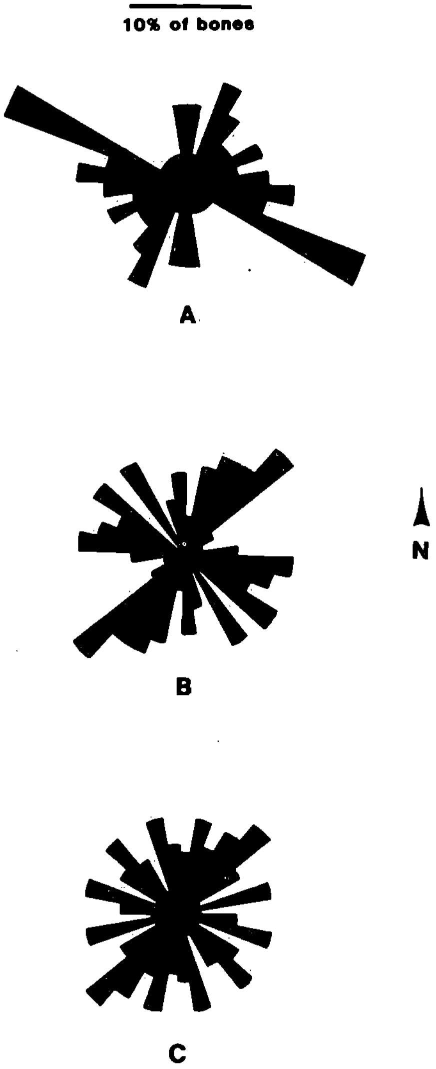

Figure 30. Rose diagrams of bearings of selected "category B" bones. (A) Calcaneum. (B) Proximal phalanx. (C) Alligator osteoderm.

paleocurrent is consistent with the orientations of solution joints within the Ocala limestones, which form along northeast/southwest axes (Williams et al. 1977). If the Thomas Farm sinkhole/cave had been connected to an underground drainage system, water would have flowed through joints in a northeasterly/southwesterly direction.

The fairly wide span of preferred orientations within each level suggests that the current was either not strong, or if strong may have been of short duration. Flow velocity in karst systems varies greatly depending on climatic conditions and height of the water table (Lane 1986). The absence of highly plunging bones also suggests that the current was not of sufficient strength to cause high degree of imbrication (Voorhies 1969), and the uniformity of low-degree dips to either the northeast or southwest indicates that once the bones were deposited, they probably were not disturbed or moved by trampling or by other biotic agents.

Sampling Duration of the Deposit

The time span of a fossil locality is a measure of the length of time that deposit has sampled the living fauna. Schindel (1980) discussed the use of sedimentation rates as a means of determining the amount of time represented within a particular locality. Behrensmeyer (1982) pointed out that a bone assemblage may accumulate over a longer or shorter span of time than the sediments in which it is deposited. For that reason, knowledge of taphonomic factors important in the formation of the bone accumulation are also important in determining the time resolution of a faunal assemblage.

Relatively little is known concerning rates of sedimentation in Florida sinkholes or caves. Evidence from other parts of the country (Laury 1980) indicates that sinkholes may fill rapidly (within 300 to 500 years). At Thomas Farm, rates of sedimentation of unit 5, the laminated sand layers (Figure 13), may be estimated. If each couplet of sand and clay laminae represents a yearly depositional cycle, this unit could have formed within a 200 year period. However, it is more likely that laminae were deposited more frequently, so 200 years represents a maximum value. Based on sedimentation rates in recent pond and lake deposits (Schindel 1980) it is not unreasonable to estimate that the Thomas Farm sediments were deposited within a 1,000 year period.

Behrensmeyer (1982) showed that bone assemblages may represent long spans of time, particularly if elements comprising the assemblage have been held in primary storage prior to final deposition. Assemblages of this type are characterized by low representations of small, light elements, and enrichment of the heaviest, densest elements. While it is possible that Thomas Farm bones may have been held in storage, lack of evidence of weathering or abrasion suggests that the majority were deposited soon after the death of the animal. Evidence that the bone source did not form over a considerably shorter time than the sediments is provided by the fact that the entire bone assemblage, at least in terms of *Parahippus leonensis*, is attritional, rather than catastrophic (Hulbert 1984).

The best evidence that the duration of the site was relatively short is provided by the stage of evolution of several of the mammalian taxa. The fact that rapidly evolving groups such as the Equidae (Hulbert 1984) and the Heteromyidae are similar in the lowermost and uppermost sedimentary levels of the site indicate that the time sampled was relative short, on the order of 1,000 years or less.

SUMMARY AND CONCLUSIONS

Depositional Environment

The presence of limestone surrounding and within the fossiliferous sediments of Thomas Farm provides convincing evidence that deposition occurred in a structure or complex of structures characteristic of karst terrains. The lack of speleothems, and the presence of both aquatic plants and aquatic vertebrates suggests that throughout most of its depositional history, the site was a sinkhole rather than a cave. Initially, the walls of the sinkhole were probably high and quite steep. The presence of a large sedimentary or debris cone within the sinkhole is indicated by the extensive and uniform dip of the sedimentary layers, and by the presence of two rubble layers composed of limestone boulders.

Source of the Bone Assemblage

Based on numerous lines of evidence, the source of the megavertebrate assemblage at Thomas Farm was almost exclusively autochthonous. Bones may have been derived primarily from two sources: from live animals that climbed or fell into the sinkhole and were either killed by the fall, or unable to make their way out, or from skeletons that accumulated and disarticulated either on the surface surrounding the sinkhole or on talus slopes along the walls of the sinkhole. In either case, modification of bone by agents such as weathering or carnivores was not a significant factor. The high degree of similarity of the compositions of the bone assemblages from the various sedimentary units to those of a complete skeleton suggest that following disarticulation, burial must have been relatively rapid, and removal or destruction of skeletal elements by various taphonomic agents did not greatly alter the assemblages. Further support for this hypothesis is provided by the fact that mammals with body masses of 15 kg or less are well-represented at the site, compared to other sites where smaller members of the fauna are under-represented due to taphonomic biases acting against their preservation (Behrensmeyer and Boaz 1980; Badgley 1986a). The numerical dominance of the three-toed horse *Parahippus leonensis* cannot be fully explained at this time. The great abundance of this taxon may have been due to its social or migratory behavior. There is little evidence to suggest that carnivores played a major role in the formation of a bone assemblage composed predominantly of one species. The site may also have functioned to some degree as a size-selective trap. Following the two limestone rubble falls, it appears that the trapping ability of the site was diminished, and the nature of the deposit was radically changed (Pratt 1989).

The presence of water-lain clays, aquatic plants, and aquatic vertebrate taxa indicates that the lower sedimentary units of the site were deposited under aquatic conditions. Although several lines of evidence, such as the lack of large aquatic frogs (Estes 1963; Pratt 1989), and the presence of *in situ* weathering in unit 8, suggest that the water was neither deep nor permanent. The lack of evidence that bones were disturbed by trampling indicates that for the most part large groups of animals did not have access to the water source. The rarity of fish and the absence of fresh-water molluscs, ostracods, and other aquatic invertebrates suggests that the site was not connected to other aquatic environments by surface streams. It is possible that water conditions may not have been suitable for some forms of aquatic life, similar to the situation noted by Laury (1980) for Hot Springs.

The presence of significant bone orientation patterns in the lower units of the site provide evidence that water within the sinkhole was not stagnant, but was moving through the sinkhole toward the southwest. The current may have been caused by artesian groundwater flow through solution joints in the Crystal River limestone. Flow velocity therefore varied with variations in the water table; however, the high representation of all but the most transportable skeletal elements indicates that flow velocity probably did not exceed 35 cm/second.

The Terrestrial Environment

Little is known concerning climates and habitats of the early Miocene of Florida. In the case of Thomas Farm, faunal evidence suggest that the region surrounding the sinkhole was forested rather than open terrain. All ungulate herbivores from the site have brachyodont dentitions, with hypsodonty indices (Janis 1984) of less than 1 (Pratt 1986). These animals, including *Parahippus leonensis*, most likely were browsers on leafy or herbaceous vegetation (Hulbert 1984). The most common carnivores found at the site are two canids with skull proportions similar to the coyote, but with extremely short limbs. Limb ratios for these carnivores are most similar to those of the South American bush-dog *Speothos venaticus* (Pratt 1986), suggesting that they were ambush hunters in wooded habitats.

The most abundant rodents of the early Miocene of Florida were quadrupedal, brachydont heteromyids most similar to the Recent forest-dwelling *Heteromys* and *Liomys*. Two species of sciurid, one an arboreal form, and the other related to *Tamias*, were also present at the site (Pratt and Morgan 1989). Spermophiline sciurids are not known from Thomas Farm. The presence of several reptile and bat taxa that today are restricted to tropical regions (Morgan pers. comm.) indicate that the climate of the region in the early Miocene was more tropical than the current climate of northern Florida. Additional evidence concerning modes of bone deposition in sinkholes and early Miocene habitats in Florida awaits further discoveries of informative early Miocene fossil localities.

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