

Taphonomy of the microvertebrate fauna from the early Miocene Thomas Farm locality, Florida (U.S.A.)

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Abstract

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In a taphonomic analysis of the microvertebrate component of the early Miocene Thomas Farm locality, north-central Florida, fossils from four sedimentary layers are analyzed and compared to determine the taphonomic factors that were involved in the formation of the bone accumulations found in the various levels of the site. The lowest layers sampled were deposited under seasonal aquatic conditions and the primary agent of bone sorting was apparently moving water. The abundant microvertebrates in the uppermost sand layer resulted from a combination of both a relatively unmodified coprocoenosis and an attritional assemblage of microvertebrates that frequented cave habitats or lived in the immediate area. Deposition within the sinkhole occurred in a relatively short span of time and the fauna is comprised primarily of those vertebrates that were living in close proximity to the sinkhole.

Introduction

The Thomas Farm locality is a well-known early Miocene (early Hemingfordian, ca. 18 Ma) vertebrate fossil deposit in north-central Florida. The site has been collected for a number of years and is known principally for its rich fauna of large vertebrates, in particular the equid *Parahippus leonensis* (Bader, 1956; Hulbert, 1984). The site and its fauna have been discussed in numerous publications. Romer (1948) and Webb (1981) both present faunal lists and literature reviews of Thomas Farm. A recent investigation (Pratt, 1986; Pratt, in press) of the taphonomy and paleoecology of the Thomas Farm has shown that microvertebrate remains are also exceedingly abundant. This paper deals with a taphonomic investigation of the microvertebrate fauna (organisms with an estimated body mass of 1 kg or less).

The most recent excavation (1981–1985) exposed a 10 m section of unconsolidated fossiliferous sediments, although most of the fossils removed in this analysis were taken from a section of approximately 3 m (Fig.1). The sediments found at the site may be grouped into three distinct types. They are, in order from lowest to highest levels:

(1) a series of alternating clay and sandy-clay layers found in the lowest exposed regions of the site (units 4–7).

(2) two massive layers of limestone boulders (units 8 and 11), separated by a thin clay (unit 10) and a sand layer (unit 9).

(3) several layers of white to yellow calcareous sand formed by the breakdown of limestone (units 12–15).

Results of preliminary sampling indicated differences in the vertebrate fossil content of the various layers. The lower units, while rich in large, or megavertebrate, remains, contain

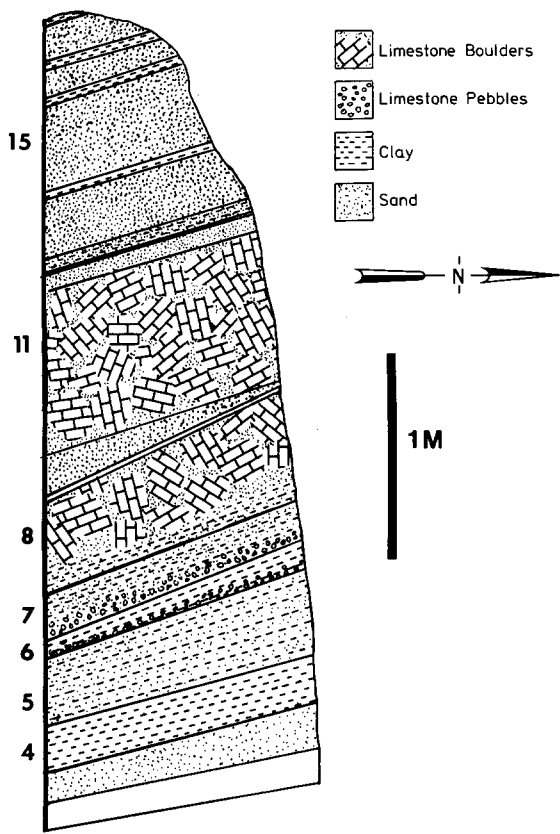


Fig.1. Composite vertical stratigraphic section showing the sedimentary levels excavated from 1981 to 1986 at the Thomas Farm locality. North to right of page.

relatively few microvertebrates; conversely, the upper limesand units are exceedingly rich in microfauna but contain little in the way of megavertebrate taxa. Both microvertebrates and megavertebrates are found in the two boulder layers. The mammalian megavertebrate fauna is dominated by two species of three-toed horse, *Parahippus leonensis* and *Archaeohippus blackbergi*. Artiodactyl remains are less common and include two camelids, two small moschids, and a protoceratid. Mammalian carnivores are represented by canids, mustelids, and amphicyonids. The reptilian component of the megafauna consists primarily of alligator and tortoise. Aquatic turtles are present but rare. The most numerous members of the microvertebrate fauna are heteromyid rodents, anurans, and bats.

This study of the microvertebrate fauna forms part of a larger analysis aimed at determination of the mode of deposition of the locality, the relevant taphonomic factors involved in the formation of bone accumulations, and a paleoecological reconstruction of the region at the time of deposition. Results of the other portions of this study (megavertebrate taphonomy and geology; see Pratt, 1986, and in press) indicate that the sediments formed a debris cone in a large, deep sinkhole in Eocene limestone. The lower clay and sandy-clay levels were apparently deposited in aquatic conditions under the influence of a slight current. The megavertebrate bones found in these layers represent an attritional assemblage. The two boulder layers formed when the sinkhole walls collapsed, events that marked the end of deposition of both the water-lain clays and the bones of large vertebrates. The upper limestone sand layers contain large numbers of microvertebrates but only fragmentary remains of larger vertebrates, and are thought to represent sediments associated with a cave environment.

The investigation of the microfaunal taphonomy was undertaken to test the depositional and ecological hypotheses produced by the geological and megafaunal analyses (Pratt, 1986, in press). The purpose of this study is twofold: first, to identify the taphonomic agents responsible for accumulation of the microvertebrate remains in the major sedimentary units, and to determine if these factors remained constant throughout the various stages of filling of the sinkhole; and second, to provide information concerning the environment of deposition and the habitat of the sinkhole and its immediate vicinity.

Thomas Farm is the only early Miocene site known to date in Florida on which an analysis of this type has been attempted. Although sites of similar age have been reported from Florida (Simpson, 1932; Frailey, 1978, 1979), fossils from these localities are not abundant, and many of the sites have been destroyed by mining or development. The information gained from this study therefore provides a

basis for paleoecological reconstruction of northern Florida during the early Miocene.

Materials and methods

Sediment collecting and processing

The fossiliferous sediments are found in a relatively level region of the site. Prior to the study, the site was surveyed and divided into 5×5 m grid squares with north/south and east/west boundaries. Most of the excavation took place within a total area of 75 m^2 . The larger grid squares were each divided into $25 \times 1 \times 1$ m squares. Square meters were selected for excavation by a stratified random technique using a random numbers table. Sediments were collected as larger bones were removed in the field. Although matrix from all identified sedimentary units (4–15; Fig.1) was collected and processed, only 4 major units from which greater than 150 kg of sediment (dry weight) had been obtained were used in the final analysis. The analysis includes two of the lower clay or sandy-clay units. The lowest well-exposed layer, unit 5 (214 kg dry weight collected) is an orange sandy-clay layer approximately 10 cm thick. Although units 6 and 7 were initially assigned two numerical designations in the field, they often proved difficult to separate. Both layers are predominantly clay units with limestone pebbles and are rich in megafauna. As the amount of sediment obtained from units 6 and 7 combined was close to 200 kg (197 kg), the microfaunal samples from these two similar units were combined for analytical purposes. Unit 11 (191 kg collected) is the upper limestone boulder layer. Composed primarily of cobble-sized boulders, this unit is rich in both megafaunal and microfaunal remains. Unit 15, the uppermost calcareous sand layer, is a massive unit rich in microvertebrates but containing only scrappy remains of large members of the fauna (191 kg used in study).

Sediment was air-dried and weighed to the nearest gram before being washed through a set of three nested screens, constructed of 4-

mesh hardware cloth (16 openings to the square to the square inch), standard 16-mesh window screen (256 openings to the square inch), and 24-mesh brass screen (576 openings to the square inch). Concentrate was picked for all identifiable bone. A binocular dissecting scope was used in the examination of the finest matrix, and bones were picked from the window-screen matrix with the aid of a magnifier or a dissecting scope.

Bones were sorted according to taxon and identified as completely as possible. Numbers of identifiable specimens of each taxon (NISP) were counted (Badgley, 1986a) and minimum numbers of individuals per taxon, or MNI (Shotwell, 1955) were calculated for each level. Raw abundances of individuals per taxonomic order were converted to relative abundances per layer to facilitate comparison of the fauna between the various layers. Relative abundances of microvertebrate taxa obtained for each unit were compared statistically with those of other units using the row by columns ($R \times C$) test of association using the G-test (Sokal and Rohlf, 1981).

Relative representations of skeletal elements (Wolff, 1973; Korth, 1979) were calculated for the two most common microvertebrates, a small heteromyid rodent, *Proheteromys floridanus*, and a toad, *Bufo praeivius*. The relative representation values of fossil rodent and frog elements from the upper sand layer, unit 15, were compared with those of elements found in modern scatalogical accumulations (Dodson and Wexlar, 1979; Korth, 1979; Pratt, 1979; Andrews and Nesbit Evans, 1983). Recent scat and pellet studies were selected based on the morphological similarity of modern predators to the carnivores and raptors known from Thomas Farm. Results were assessed statistically using an $R \times C$ test for association and the Spearman coefficient of rank-order correlation (Sokal and Rohlf, 1981).

Fossil microfaunal elements were examined under high magnification of a binocular dissecting scope. Breakage of bones was assessed as resulting from either pre-fossilization or post-fossilization factors, based on descriptions

in Behrensmeyer (1978), Korth (1979), Hill (1980), Shipman (1981), and Binford (1981). Fossil bones that showed pre-fossilization breakage or evidence of acid destruction were compared, with the aid of either a dissecting scope or SEM, to Recent bones from scats of the mammalian carnivores *Canis latrans*, *Lynx rufus*, and *Mustela frenata*, from pellets of the raptors, *Tyto alba*, *Bubo virginianus*, *Otus asio* and *Buteo jamaicensis*, and to bones experimentally abraded in a rock polisher (Pratt, 1979). Quartz grain equivalents were computed for major elements of modern *Peromyscus* and *Rana* as a means of predicting hydraulic behavior of microvertebrate elements (see Appendix I). The equivalent quartz diameter (dq_e) indicates the size of the quartz grain that achieves the same terminal settling velocity as the bone in question and hypothetically would be transported at a current velocity similar to that required to move the element (Behrensmeyer, 1975; Korth, 1979). As most microvertebrate bones from the site were broken, quartz grain equivalents were determined for those portions of bones most frequently recovered (>50% representation) rather than for complete limb bones. Bones were immersed in water until waterlogged (1–3 days), then dropped individually into a graduated cylinder 65 cm in height filled with room-temperature water. Each bone's rate of descent through standing water was timed with a stopwatch accurate to 0.01 s. Bones were allowed to fall for 15 cm before timing began, and the mean fall velocity, in cm/second, was determined from 10 trials with each bone. The equation for calculating the equivalent diameter is

$$dq_e = 0.000928 v_s^2$$

where dq_e is the diameter of the equivalent quartz grain, in centimeters, and v_s is the settling velocity of the skeletal element (Behrensmeyer, 1975). Bones were assigned to sorting groups based on their predicted transport potentials in running water (Voorhies, 1969; Dodson, 1973; Behrensmeyer, 1975; Korth, 1979; Pratt, 1979).

Taphonomic models

The majority of microvertebrate bone accumulations are frequently described as either coprocoenoses or fluvial deposits. Coprocoenoses (Mellet, 1974) are accumulations composed of bony remains derived from carnivore scat. A fossil coprocoenosis may be identified by comparison of a microvertebrate fossil assemblage with Recent fecal accumulations of mammalian predators or pellet accumulations of raptorial birds (Mellet, 1974; Korth, 1979; Dodson and Wexlar, 1979; Maas, 1985). An ideal modern comparative sample contains remains deposited by several individuals of a single species, with large sample sizes of prey items. Large samples minimize the individual variation in feeding behavior and digestive processes. Unfortunately, although modern scatological analyses have been undertaken by a number of workers, sample sizes for any one species are still low and variation between studies in terms of prey and skeletal content of fecal accumulations is often very high.

In testing a fossil accumulation for evidence of a coprocoenosis, a basic knowledge of the fossil fauna is also necessary, particularly if the proposed sources of the accumulation are extinct carnivores. The size range of the potential prey items should be determined, and the investigator should be familiar with the numbers and types of predators that could have been involved in the formation of the coprocoenosis. At Thomas Farm, the dominant microfaunal remains are those of a small heteromyid rodent (*Proheteromys floridanus*) that weighed about 10 g (Pratt, 1986). The most common mammalian carnivores were two canids, *Cynodesmus iamonensis* and *Tomarctus canavus*, both similar in size cranially to modern coyotes and jackals but postcranially rather short limbed (Pratt, 1986). The body mass of the smaller form, *T. canavus*, ranged from 7 to 11 kg, while the larger *C. iamonensis* was about 12–17 kg (Pratt, 1986). Based on studies of food habits of Recent canids of similar size (Rosenzweig, 1966; Ewer, 1973; MacDonald, 1977; Litvaitis and Shaw, 1980;

Yearsley and Samuel, 1980; Bekoff, 1982; Samuel and Nelson, 1982; MacCracken and Uresk, 1984; McShane and Grettenberger, 1984; Toweill and Anthony, 1988), it is most likely that the diet of these two species would have been predominantly small rodent-sized (i.e., mouse-sized) mammals. A badger-like mustelid, *Leptarctus ancipidens*, (mass about 5 kg) was also fairly common, as were two species of small weasel-like forms, *Miomustela* sp. and an undescribed species (estimated body mass about 1 kg). It is likely that these species also were capable of taking small rodents and other small vertebrates as prey, much as modern mustelids do today (Erlinge, 1975; Tapper, 1976; Soutiere, 1979; Godin, 1982; Linscombe et al., 1982; Strikland et al., 1982a, b; Svendsen, 1982; Blandford, 1987). The larger mammalian carnivores from Thomas Farm, the amphicyonid *Amphicyon longiramus* and the ursid *Hemicyon johnhenryi* both exceeded 20 kg in body weight (Pratt, 1986) and probably routinely took larger prey than the small rodents known from the site. Remains of the small amphicyonid *Cynelos caroniavorus* are extremely uncommon, and little is known about its morphology and possible food habits.

Avian predators known from the site include three species of the kite *Promilio* (Brodkorb, 1956; Wetmore, 1958) and several as yet undescribed hawks (Becker, 1987; pers. comm., 1987), whose Recent relatives cast bone-containing pellets. Owls, the most prolific accumulators of microvertebrate bones, are not known from Thomas Farm.

Evidence for fluvial deposition of vertebrate accumulations is usually based at least in part on geologic factors (Voorhies, 1969; Behrensmeyer, 1975, 1988; Korth, 1979; Badgley and Behrensmeyer, 1980). Most studies on microvertebrate bone transport have been performed on localities where fluvial effects are undoubtedly of overwhelming significance (Wolff, 1973; Korth, 1979). At the Thomas Farm locality there is no clear indication of a fluvial system in the classic sense. However, the possibility that the assemblage has been modified to some degree by moving water will be

investigated, as megafaunal evidence strongly indicates that the lower sedimentary units were deposited under aquatic conditions (Pratt, 1986). In addition to the previously mentioned agents of bone concentration, recent studies by Shipman and Walker (1980) have shown that certain species of African ants accumulate bones of very specific sizes.

Other prefossilization taphonomic factors such as preburial exposure can modify an assemblage by causing loss of skeletal remains. Surface exposure is no doubt of importance in attritional faunal assemblages (Korth, 1979; Behrensmeyer et al., 1979; Behrensmeyer and Boaz, 1980; Bown and Kraus, 1981). Remains of the smallest members of the fauna are subject to the greatest degree of destruction due to their high surface area to volume ratios, and because porous bones are likely to be destroyed more readily than compact bones. This type of loss is most important if relative abundances of megavertebrates and microvertebrates are directly compared. Little quantitative data exists on relative destruction rates of skeletal elements of microvertebrates. For the purposes of this study, it is assumed that weathering effects have acted more or less equally on the microvertebrate remains. Although it is likely that the smallest, least dense elements would be lost most rapidly, the lack of physical features indicative of weathering suggests that sub-aerial exposure played a relatively minor role in modifying the microvertebrate assemblage.

The agent responsible for a microfaunal accumulation can in many cases be determined by examination of three features: physical condition of bones, faunal composition, and relative representations of skeletal elements. Bone orientation, an important factor in determining the taphonomic history of megavertebrate assemblages, is not routinely used in analysis of microvertebrate accumulations.

Physical modification or chemical destruction of bone includes breakage and fracture resulting from a predator's method of feeding (Mellett, 1974; Dodson and Wexlar, 1979; Korth, 1979; Pratt, 1979; Andrews and Nesbit

Evans, 1983) and the effects of stomach acid on tooth enamel and bone (Mayhew, 1977; Fisher, 1981a-c; Andrews and Nesbit Evans 1983). Many of these features can only be discerned by microscopic or SEM analysis. Preferential destruction of one portion of a bone may also be characteristic of damage caused by a particular type of carnivore.

Physical destruction also results from abrasion and breakage caused by water-borne sand particles. Although this type of damage may be readily identified on large bones, it is usually difficult to discern on microvertebrate elements. Korth (1979) and Pratt (1979) performed experimental abrasion studies on small mammal remains, and showed that bones of microvertebrates are modified by water and sand wear. In highly energetic fluvial systems, only the most durable portions of small bones remain.

Faunal composition refers to the species of microvertebrates found in a deposit and their relative abundances. The predominance of microvertebrates of a certain size range or the numerical dominance by one or two species can indicate that an accumulation was formed by a carnivore (Maas, 1985). Mammalian and avian predators are both known to exhibit preferences for certain prey types, or a specific size range of prey (Rosenzweig, 1966, 1968).

Little is known concerning the expected taxonomic diversity of microfauna represented in a fluvial deposit. The presence of a species in a stream deposit is more likely to be a function of chance rather than its being the preferred or non-preferred prey item of a particular predator. Unless a fluvially-deposited accumulation is initially derived from a coprocoenosis, species diversity and equitability would probably be greater than that seen in a coprocoenosis. In addition to terrestrial vertebrates, those species normally found in fluvial or other aquatic environments (for example, fish) should be well-represented in a fluvial fossil deposit (Voorhies, 1969; Behrensmeyer, 1975; Webb et al., 1981; Hook and Baird, 1986; Hook and Ferm, 1988).

Bone relative representations (Wolff, 1973; Korth, 1979) provide a diagnostic means of determining the source of a microvertebrate accumulation. Elements may be selectively discarded or characteristically destroyed by carnivores, and will therefore be underrepresented in a coprocoenosis. Preservation ratios of skeletal elements can also provide evidence that an assemblage has been sorted by running water if the most highly represented elements possess similar hydrodynamic properties (Voorhies, 1969; Behrensmeyer, 1975; Korth, 1979; Hanson, 1980). The types and number of bones represented are in part dependent on current speed and the distance the element has been transported (Hanson, 1980).

Results and discussion

Sample size

The sample size of a microfaunal assemblage is a function of the amount of sediment, by dry weight, that is processed to obtain microvertebrate taxa. The volume of matrix that must be washed in order to recover a sample of microfauna is dependent on the richness of the matrix, and therefore varies from site to site. Fortunately, even the most depauperate sediments at Thomas Farm contain microvertebrate remains in fairly high abundances (over 3 identifiable specimens per kg dry weight of matrix).

It is difficult to determine if a given amount of sediment adequately samples the microfauna present. A general assessment may be made by plotting the cumulative number of taxa obtained in serially collected samples of known weight taken from a particular layer or locality. When the curve approaches an asymptote, it is inferred that the majority of species that are present in the deposit have been collected (Wolff, 1975). Comparison of cumulative curves for different collecting sites within a locality not only indicates if sample sizes are adequate, but may also provide evidence of

similarities or differences in faunal content between the samples.

In units 5, 6-7, and 11, the recovery of microvertebrate taxa reaches an upper limit of about 34 species, with the curves becoming asymptotic at about 160 kg (dry weight) of matrix (Fig.2). The total number of microvertebrate species known from Thomas Farm, (including several undescribed taxa), is 51. Species recovery is therefore 66% in these units. The curve for unit 15 becomes asymptotic at about 185 kg, with a representation of microfaunal taxa of about 78% (Fig.2). Several of the taxa found in unit 15 are those considered to be very rare, and the overall numbers of specimens recovered are far greater than those of any other unit. The similarity of the shape of the curves for the lower sedimentary layers (5 and 6-7) not only indicates that microfauna sample sizes are large enough to permit comparisons between layers, but also shows that in terms of microfaunal taxa, the lower layers are of similar richness, while unit 15 is considerably more productive.

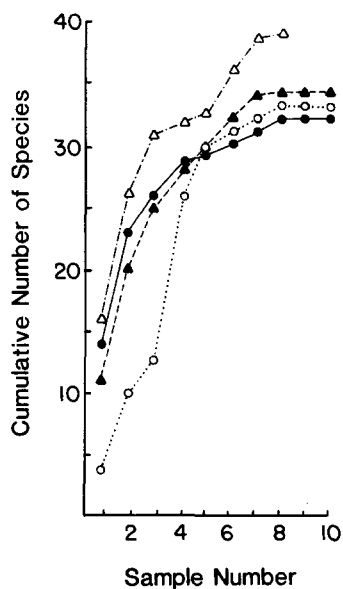


Fig.2. Graph depicting cumulative numbers of microvertebrate species obtained from serially collected matrix samples. Approximate weight of each sample = 20 kg. Open triangles, unit 15; open circles, unit 11; closed circles, unit 6/7; closed triangles, unit 5.

Physical modification of bone

Unit 15

Many elements of the small heteromyid *Proheteromys floridanus* show evidence of breakage and acid destruction similar to that caused by predators. Features indicative of water wear are not apparent, although evidence of fluvial abrasion is often difficult to discern on broken microvertebrate elements.

The condition of rodent incisors provides evidence of ingestion by a carnivore (Fig.3). The effect of acid on rodent incisors was first pointed out by Mayhew (1977), who showed that incisors regurgitated by hawks have undergone this distinctive type of modification. Both hawks and mammalian predators that ingest their prey cause similar types of rodent incisor modification (Fig.3B, C, E) including both loss of enamel and exfoliation or solution of the dentine at the occlusal end of the tooth. These features are also seen on rodent incisors collected from unit 15 (Fig.3A). In contrast, incisors ingested and regurgitated by Barn Owls are relatively intact (Fig.3D), and rodent incisors abraded in a tumbling barrel with a water-sand slurry (Fig.3F) are rounded but do not show complete enamel loss or removal of dentine layers (Korth, 1979; Pratt, 1979).

Many of the rodent cheekteeth from unit 15 have also have corroded enamel, which is powdery in appearance. The occlusal surface of the tooth, particularly around worn cusps, may be destroyed. Fluvial abrasion can also cause cusp destruction, but the enamel of abraded teeth appears shiny and the roots are often broken off or worn away. Acid-etched teeth usually possess complete roots, as the portion of the tooth located below the gum line remains intact (Mayhew, 1977). Teeth that have fallen out of the jaw or skull during digestion also possess roots, but the roots often have a whittled shape caused by acid digestion. Large numbers of rodent teeth from Thomas Farm unit 15 have this appearance.

Many of the postcranial elements of *Pro-*

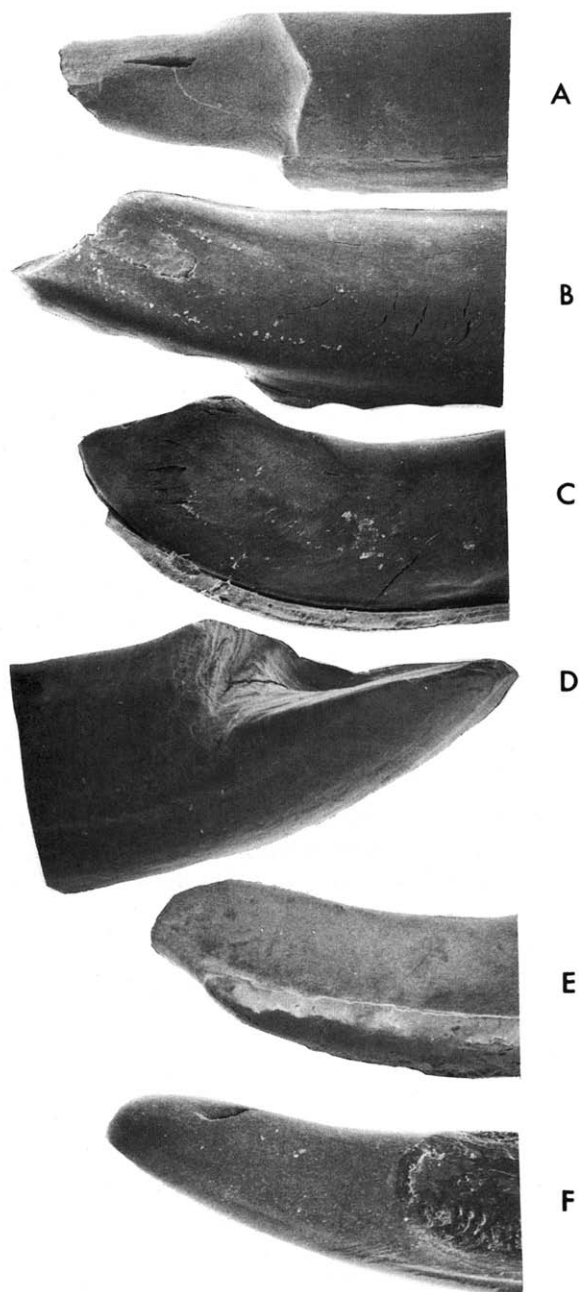


Fig. 3. SEM photographs showing surface features of fossil and Recent rodent incisors. A. *Proheteromys floridanus*, unit 15 Thomas Farm. B. Small rodent from coyote scat. C. Small rodent from weasel scat. D. *cf. Microtus* from Barn Owl pellet. E. *Mus* from Red-Tailed Hawk pellet. F. Small rodent incisor abraded experimentally with a sand/water slurry in a rock polisher for two weeks.

heteromys floridanus in unit 15 possess sharp fractures characteristic of pre-depositional breakage (Korth, 1979; Hill, 1980; Shipman, 1981). Some of the broken edges appear smoothed and rounded, presumably the result of acid digestion (Mayhew, 1977; Andrews and Nesbit Evans, 1983), although fluvial polishing can also smooth sharp edges. The degree of breakage and amount of acid wear on these small bones appears most consistent with that caused by some canids and large mustelids (Andrews and Nesbit Evans, 1983). Weasel-sized mustelids reduce most bones of even very small prey to minute shards (Gamberg and Atkinson, 1988). Among avian predators, Barn Owls inflict the least damage on rodent bones, while strigid owls tend to cause more breakage (Dodson and Wexlar, 1979; Pratt, 1979). Prey elements ingested by hawks are broken before they are swallowed (Clark, 1972; Mayhew, 1977; Pratt, 1986).

Another important aspect of skeletal element preservation is the portion of the bone (complete, proximal end, distal end) that is represented in a fossil assemblage. Bones that have passed through a predator's digestive tract may show differential survival of one end over another. Table I lists the relative preservations of ends of selected limb bones of *Proheteromys floridanus* from unit 15. Complete bones are very rare, and most of the long bones consist of a portion of the shaft and one articular end. The preservation ratios of fossil elements are compared with those for broken bones taken from scat and pellets of mammalian and avian predators (Dodson and Wexlar, 1979; Andrews and Nesbit-Evans, 1983). A Chi-Square goodness of fit test shows that relative preservation of two of the three limb bone types from mongoose or fox scat (Andrews and Nesbit Evans, 1983) are not significantly different at the $p=0.01$ level from those in the fossil sample while end preservation proportions of all three elements from coyote scat and pine martin scat (Andrews and Nesbit Evans, 1983) are significantly different from the fossil rodent remains. Higher percentages of complete long bones are found in coyote and mongoose

TABLE I

End preservation ratios of selected limb bones of *Proheteromys floridanus* from unit 15 compared to end preservation ratios of small mammal bones from predator scat or pellets. Percent complete refers to percentage of total that are unbroken. Percentage proximal or distal calculated as ratio of total number of broken bones possessing articular ends. Comparative data for coyote, fox, mongoose from Andrews and Nesbit Evans (1983), comparative data for owls from Dodson and Wexlar (1979). Abbreviations: G-H = Great Horned.

	Unit 15	Coyote	Fox	Mongoose	Barn Owl	G-H Owl	Screech Owl	Red-Tailed Hawk
<i>Humerus</i>								
% Complete	0	7	0	30	89	63	13	0
% Proximal	25	50	17	48	67	69	60	0
% Distal	75	50	83	52	33	31	40	100
<i>Femur</i>								
% Complete	0	0	0	25	100	72	47	0
% Proximal	68	54	62	69	0	32	29	92
% Distal	32	46	38	31	0	68	71	8
<i>Tibia</i>								
% Complete	0	0	0	37	74	5	11	0
% Proximal	37	90	67	40	20	80	33	shafts
% Distal	63	10	33	60	80	20	67	only

scat than are seen in the fossil sample (Andrews and Nesbit Evans, 1983). Bones from raptor pellets show few similarities to the fossil elements with regards to preferred end preservation. Most of the limb bones of small rodents found in Great-Horned Owl and Barn Owl pellets are whole, and those that are not show opposite preferred end preservations to those of the fossil remains (Dodson and Wexlar, 1979). My investigations of Recent raptor pellets indicate that elements from Screen Owl and hawk pellets are seldom complete. Bones that have been ingested by hawks usually have one articular end preserved with a much higher frequency over the other end (Table I).

Bones of the toad *Bufo praeivius* are also very numerous in unit 15. Many of the elements show signs of destruction indicative of carnivore ingestion. The bones most frequently found broken show similar breakage patterns to anuran bones recovered from Barn Owl pellets (Morgan, 1977). Over 90% of the bones of fossil *Bufo* found in the unit 15 matrix sample are broken. Of the elements examined in this study, scapulae are the only elements frequently found whole. Most humeri are

missing the proximal half, the radio-ulna is represented primarily by the proximal end, and the urostyle consists of the posterior articular portion. The lateral processes are usually broken off the sacrum, and the ilium consists of the acetabulum and up to one-third of the ilial shaft. The same types of elements recovered from Barn Owl pellets (Morgan, 1977) collected on Cayman Brac were found whole roughly 60% of the time, with the exception of the scapula, of which 94% of the specimens were whole. If the large numbers of toad remains found in unit 15 were accumulated by a predator, the animal responsible, either a mammal or perhaps an avian predator such as a kite, evidently caused a higher degree of bone breakage than does a Barn Owl. Recent kites, Screech Owls, and Burrowing owls are known to feed on anurans (May, 1935; Karalus and Eckert, 1974); however, analysis of pellets that contain anurans is needed before definite conclusions can be drawn concerning the source of the fossil toad remains. It is also possible that remains of toads were deposited by a mammalian predator, as several types of mammalian carnivores are known to feed on

toads and frogs (Ewer, 1973; Godin, 1982; Linscombe et al., 1982). It has been reported that the polecat *Mustela putorius*, frequently preys on toads, consuming all but the cranial region that contains the poison glands (Blandford, 1987). However, no quantitative data are yet available on non-mammalian skeletal remains in mammalian predator scat.

The elements of other microvertebrate species (bats, birds, reptiles) in the unit 15 sample show little evidence either of ingestion by carnivores or of fluvial abrasion. Many of the bat specimens are in excellent condition; complete dentaries with teeth, and limb bones are often found. Few bat cheekteeth show evidence of acid corrosion, indicating these animals either were not prey items, or that their bones were ingested by a predator whose method of feeding caused minimal bone destruction. Birds and reptiles are among the least common vertebrate groups in unit 15 (Table II) and the remains of these animals are often too fragmentary to examine for evidence of predator damage. Coyotes, jackals, foxes, and several species of mustelid prey on birds and infrequently, reptiles. In most cases, birds represent from about 4% to 10% of the diet (Erlinge, 1975; Tapper, 1976; Frank, 1979; Soutiere, 1979; Harris, 1981; Strickland et al., 1982a; MacCracken and Uresk, 1984; McShane and Grettenberger, 1984; Avery et al., 1987; Toweill and Anthony, 1988), but at certain times of the year, avian prey may comprise nearly 20% of the diet of some species (Litvaitis and Shaw, 1980). Some of the fossil bird bones recovered are in extremely good condition considering their fragility. Bird bones obtained from Recent Barn Owl pellets are almost always complete, while those from Great-Horned Owl and Screech Owl pellets are most often broken and may be corroded on the ends. Bird skeletal remains ingested by Recent hawks are usually subject to extensive acid destruction (Errington, 1933; Clark, 1972; Mayhew, 1977).

Units 11-5

About 30% of the rodent elements from the boulder layer, unit 11, show evidence of

TABLE II

Relative abundances of microfaunal taxa from Thomas Farm

Level and taxon	Number of specimens	Percent of total	MNI	Percent of total
<i>Unit 15</i>				
Osteichthyes	1	0.01	1	0.2
Urodela	53	0.8	5	1.2
Anura	1217	17.9	174	42.2
Squamata	412	6.1	43	10.4
Aves	51	0.8	9	2.2
Chiroptera	274	4.1	19	4.6
Insectivora	2	0.03	1	0.2
Rodentia	4776	70.2	160	38.8
Total	6786	100.0	412	100.0
<i>Unit 11</i>				
Osteichthyes	3	0.2	1	0.7
Urodela	4	0.3	1	0.7
Anura	260	15.6	46	30.5
Squamata	118	7.1	13	8.6
Aves	35	2.1	6	3.9
Chiroptera	93	5.6	6	3.9
Rodentia	1159	69.2	78	51.6
Total	1672	100.0	151	100.0
<i>Unit 6-7</i>				
Osteichthyes	8	1.1	2	1.8
Urodela	54	8.7	5	4.5
Anura	246	39.1	54	48.6
Squamata	61	9.7	16	14.4
Aves	16	2.5	5	4.5
Chiroptera	49	7.8	5	4.5
Insectivora	3	0.5	1	0.9
Rodentia	197	31.3	23	20.7
Total	634	100.0	111	100.0
<i>Unit 5</i>				
Osteichthyes	4	0.4	1	0.6
Urodela	215	20.8	13	8.6
Anura	376	36.7	87	57.6
Squamata	127	12.4	17	11.2
Aves	4	0.4	3	2.0
Chiroptera	35	3.4	6	3.9
Rodentia	264	24.3	24	15.9
Total	1025	100.0	151	100.0

carnivore-induced bone damage, although the majority of bones from this unit do not. In the lower clay layers 5 and 6-7, very few of the rodent incisors or cheekteeth clearly show evidence of carnivore destruction or water wear. Limb bones of microvertebrates are rare in these units, and those recovered are very fragmentary. The relative rarity of bones

possessing surface features that are indicative of carnivore-caused destruction does not rule out the possibility that the microfauna found in the lower units of the site was originally derived from a predator accumulation, but does suggest that other taphonomic factors could have formed or modified the original bone accumulation.

Faunal composition

Faunal diversity and composition can provide useful taphonomic information concerning taphonomic events, in addition to indicating depositional environment and local

habitats. Table II lists both raw and relative abundances of microvertebrates from Thomas Farm. Faunal diversity within each of the major layers is shown graphically in Fig.4.

In considering microfaunal abundance and diversity in terms of numbers of identifiable specimens, it is immediately evident that a 200 kg sample of matrix from the upper layer unit 15 contains higher numbers of microvertebrate specimens than do comparable samples from any of the other sedimentary units (Table II). Proportions of specimens per order, especially of rodents and anurans, appear most similar between units 5 and 6-7. These lower units differ from the upper layers 11 and 15, in

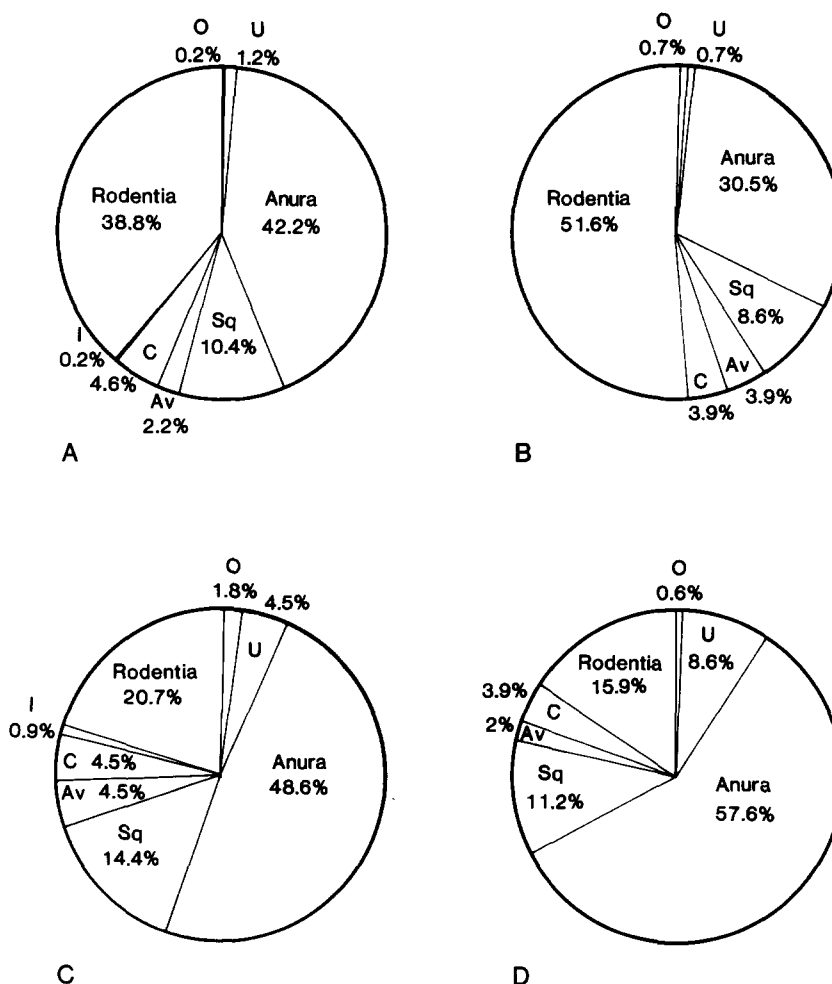


Fig.4. Relative abundances of microfaunal taxa at Thomas Farm. A. Unit 15. B. Unit 11. C. Unit 6-7. D. Unit 5. Abbreviations: Av=Aves; C=Chiroptera; I=Insectivora; O=Osteichthyes; Sq=Squamata; U=Urodela.

which approximately 70% of the identifiable specimens belong to rodents. If the data are examined statistically using the $R \times C$ test of association using the G-test (Sokal and Rohlf, 1981), the relative abundances of specimens per order in each unit (Table IIIA) are significantly different from those in the other units examined ($p \leq 0.01$).

Unlike the relative number of specimens, the relative abundances in terms of MNI per order between the various layers do not appear very different (Fig. 4). Statistics (Sokal and Rohlf, 1981, p. 599) indicate that relative abundances of individuals per order in unit 15 are not significantly different from those of unit 11, but both units 15 and 11 are different from units 6–7 and 5 (Table IIIB). Unit 6–7 and 5 are also similar to one another in terms of faunal relative abundances based on MNI (Table IIIB). These results suggest that abundance values based on numbers of specimens overestimate the differences between layers, while values based on MNI evidently underestimate differences. However, estimates based on MNI are probably more accurate for several reasons.

TABLE III

Statistical comparison of faunal composition of different stratigraphic units from Thomas Farm (Table II). Reported are calculated G values from the $R \times C$ test for association (Sokal and Rohlf, 1981, p. 599). Values greater than 18.5 indicate significant differences at $p \leq 0.01$ (d.f. = 7)

Unit	Unit		
	15	11	6–7
A. Number of specimens per order			
11	47.6	—	—
6–7	474.4	369.2	—
5	1153.2	792.2	86.6
Unit	Unit		
	15	11	6–7
B. MNI per order			
11	11.4	—	—
6–7	161.3	31.3	—
5	333.6	55.6	6.7

First, there is a high likelihood of original association of the elements, and second, there is no clear indication of fluvial transport, conditions that Badgley (1986a, b) notes as being better suited to abundance calculations based on MNI. Minimum numbers of elements (MNE; Badgley, 1986b) were calculated for one sample, but as these values were extremely similar to NISP, they were not used. Regardless of the method of estimating abundances, the microvertebrate fauna in unit 15 is unlike any of the lower units in both numbers and proportions of specimens and individuals per order. The large numbers of microvertebrate specimens found in unit 15, 35.5 identifiable specimens per kg, compared to 4.8 identifiable specimens per kg in unit 5, and 3.2 in unit 6–7, and the numerical dominance of the small vertebrates *Proheteromys floridanus* and *Bufo praeivius*, suggest a bias indicative of a carnivore-formed accumulation. However, based on faunal composition alone, it is not possible to identify the specific type of coprocoenosis represented. It is known that modern mammalian carnivores may select particular types and sizes of prey (Rosenzweig, 1966, 1968; Ewer, 1973) although prey choice may vary individually, regionally, or seasonally (Lockie, 1959; Ewer, 1973; Erlinge, 1974; 1975; Tapper, 1976; MacDonald, 1977; Berg and Chesness, 1978; Frank, 1979; Soutiere, 1979; Yearsley and Samuel, 1980; Linscombe et al., 1982; Strickland et al., 1982a, b; Svendsen, 1982; MacCracken and Uresk, 1984; McShane and Grettenberger, 1984; Towell and Anthony, 1988). Avian predators also exhibit a great deal of variation in the type and numbers of prey consumed. For example, Barn Owls in Florida feed primarily on field mice, cotton rats, and shrews (Trost and Hutchison, 1963), while their West Indian counterparts often take frogs and lizards as the mainstay of their diets (Morgan, 1977). Barn owls in urban areas feed predominantly on rats (Morris, 1979). The problems associated with regonizing a coprocoenosis solely on the basis of faunal composition are compounded by the fact that an accumulation of fossil bones is rarely a pure coprocoenosis. It

is possible for a bone assemblage to be formed by several types of carnivores, or a combination of a coprocoenosis and an attritional or fluvially-sorted assemblage. Unit 15 contains microfaunal taxa that appear to have been accumulated by a carnivore, but also contains other groups, such as bats and lizards, that may not have been prey items.

Identifying a fluvial or water-mediated accumulation based on faunal composition alone is also difficult. Few studies exist that contain reference to relative abundances of the entire microvertebrate fauna in fluvially-lain sediments. The majority of published studies deal solely with the micromammalian taxa, for example, the Pleistocene Rodeo Ranch locality in California (Wolff, 1973).

A striking feature of the Rodeo fauna is the high diversity of small mammals, particularly rodents. It is possible that a high diversity of taxa is characteristic of a fluvial deposit that samples a wide range of habitats, as opposed to a sinkhole or a trap that samples a fairly limited area.

One characteristic that distinguishes the Thomas Farm microvertebrate fauna from that of most fluvial localities is the presence of large numbers of bats, particularly in unit 15 (Tables II and IV). Bats are extremely rare in most fluvial sites, even in north Florida Miocene fluvial deposits that are found in karst regions where caves were undoubtedly abundant. Only one bat fossil (a distal radius) has been reported from the fluvially-deposited late Miocene Love Site (Webb et al., 1981), although large amounts of matrix were picked for microfauna.

The differences in faunal composition between the upper sand unit 15 and the lower clay units (5, 6-7) become more evident if the fauna is examined below the ordinal level. Rodent specimens are far less numerous in the lower layers (Tables II and IV), while the diversity of anurans is greater in these levels than in the upper units 11 and 15 (Table V).

Table V lists abundances of amphibian species, by MNI, found in each major sedimentary unit. In addition to higher numbers of the

TABLE IV

Relative abundances of micromammalian taxa from Thomas Farm

Taxon and level	Number of specimens	Percent of total	MNI	Percent of total
<i>Unit 15</i>				
<i>Limnoecus</i> n. sp.	2	0.03	1	0.6
Chiroptera	274	5.7	19	10.5
<i>Proheteromys floridanus</i>	4666	92.3	157	87.2
<i>P. magnus</i>	2	0.03	1	0.6
<i>Nototamias hulberti</i>	6	0.12	2	1.1
<i>Unit 11</i>				
Chiroptera	93	7.4	16	7.1
<i>P. floridanus</i>	1150	91.8	73	86.9
<i>P. magnus</i>	5	0.4	2	2.4
<i>Nototamias hulberti</i>	1	0.08	1	1.2
<i>Petauristodon pattersoni</i>	1	0.08	1	1.2
Eomyidae	2	0.16	1	1.2
<i>Unit 6-7</i>				
<i>Limnoecus</i> n. sp.	3	1.2	1	3.4
Chiroptera	49	19.9	5	17.2
<i>P. floridanus</i>	171	68.6	17	58.6
<i>P. magnus</i>	12	4.9	2	6.8
<i>Nototamias hulberti</i>	3	1.2	1	3.4
<i>Petauristodon pattersoni</i>	11	4.5	3	10.3
<i>Unit 5</i>				
Chiroptera	35	11.7	6	20.0
<i>P. floridanus</i>	248	82.9	18	60.0
<i>P. magnus</i>	9	3.0	2	6.7
<i>Nototamias hulberti</i>	2	0.7	1	3.3
<i>Petauristodon pattersoni</i>	3	1.0	2	6.7
Eomyidae	2	0.7	1	3.3

aquatic salamander *Notophthalmus*, relative abundances of frog species in unit 5 are the least similar to those of any of the other layers, with a small ranid being the most common amphibian. Bufonids, which dominate the herpetofauna in all other units by more than 2 to 1 over the next most common anuran, are the third most abundant taxon in unit 5. *Rana* specimens are dominant in unit 6-7, but rare in units 11 and 15. *Acris barbouri* is also common in units 5 and 6-7, but is not well-represented in the upper layers. Relative abundances of the treefrog *Hyla goini* are fairly uniform through-

TABLE V

Relative abundances of amphibians from Thomas Farm

Taxon and level	MNI	Percent of total MNI
<i>Unit 15</i>		
<i>Scaphiopus</i> sp.	1	0.6
<i>Bufo praeivius</i>	123	68.7
<i>Hyla goini</i>	28	15.6
<i>Hyla miosfloridana</i>	1	0.6
<i>Hyla</i> sp.	1	0.6
<i>Acris barbouri</i>	8	4.5
<i>Rana abava</i>	12	6.7
<i>Notophthalmus robustus</i>	3	1.7
<i>Siren</i> sp.	1	0.6
<i>Batrachosauroides</i> sp.	1	0.6
<i>Unit 11</i>		
<i>Bufo praeivius</i>	31	65.9
<i>Hyla goini</i>	13	27.6
<i>Acris barbouri</i>	1	2.1
<i>Rana abava</i>	1	2.1
<i>Notophthalmus robustus</i>	1	2.1
<i>Unit 6-7</i>		
<i>Bufo praeivius</i>	29	49.1
<i>Hyla goini</i>	9	15.2
<i>Hyla</i> sp.	1	1.7
<i>Acris barbouri</i>	6	10.2
<i>Rana abava</i>	7	11.8
<i>Rana bucella</i>	2	3.4
<i>Notophthalmus robustus</i>	4	6.7
<i>Siren</i> sp.	1	1.7
<i>Unit 5</i>		
<i>Scaphiopus</i> sp.	1	1.0
<i>Bufo praeivius</i>	14	14.0
<i>Hyla goini</i>	18	18.0
<i>Hyla</i> sp.	2	2.0
<i>Acris barbouri</i>	14	14.0
<i>Proacris mintoni</i>	1	1.0
<i>Rana abava</i>	32	32.0
<i>Rana bucella</i>	5	5.0
<i>Notophthalmus robustus</i>	12	12.0
<i>Siren</i> sp.	1	1.0

out all layers. The $R \times C$ test of association shows that the relative abundances of amphibian species in units 5 and 6-7, although significantly different from one another at the $p \leq 0.01$ level (Table VI) are more similar to one another than either is to any other layer. Numbers of anurans in unit 11 are too low to

TABLE VI

Statistical comparison of amphibian faunal composition (MNI) of different stratigraphic units from Thomas Farm (Table V). Reported are calculated G values from the $R \times C$ test for association (Sokal and Rohlf, 1981, p. 599). Values greater than 20.09 are significantly different at $p \leq 0.01$ (d.f. = 8)

Unit	Unit	
	15	6-7
6-7	46.2	—
5	106.2	27.2

allow for statistical comparison. The variation in representation of frog species between the layers can be explained by minor habitat and depositional differences acting at the time of formation of the various layers. *Rana abava* probably preferred aquatic conditions. Although ranids today are known to occur within a wide variety of habitats, those that possess an ilium morphology similar to that of the Thomas Farm species are strong swimmers and are most frequently found in aquatic environments (Pratt, in prep.). Living species of *Acris* are also commonly found in or near aquatic habitats (Conant, 1975; Ashton and Ashton, 1988), and it is possible that the fossil taxon may have exhibited such a preference. The predominance of these forms over the presumably terrestrial toad *Bufo praeivius* in units 5 and 6-7 indicates that aquatic conditions must have been present at least on a temporary or periodic basis while these sediments were being deposited, unlike conditions in the upper units 11 and 15.

Although the microvertebrate fauna indicates that different taphonomic factors may have been involved in the formation of the bone deposits in the upper and lower units of the site, overall taxonomic similarity provides information concerning the sequence of deposition and the environment of the region surrounding the sinkhole. Bony fish, marsupials, and insectivores are rare throughout all levels of the site (Table II). Fish are represented by

small, isolated vertebrae that cannot be identified below the ordinal level (S. Scudder, pers. comm., 1986). The low representation of fish at the Thomas Farm contrasts sharply with the numbers found at fluvially deposited sites in Florida such as the Love Site (Webb et al., 1981). The large numbers of other microvertebrates found in the Thomas Farm sediments and their fine state of preservation suggests that the lack of fish remains is not due to preservational bias. Rather, the rarity of fish provides evidence that water within the sink was derived from an ephemeral, rather than permanent source and that the sinkhole was not fed by large, aboveground streams or outlets. The significance of the low representation of marsupials and insectivores is not clear. The marsupial is known from one tooth. Insectivores are usually rare in microvertebrate deposits unless they have been accumulated by an avian predator such as an owl (Southern, 1969; Pratt, 1979).

Microfaunal taxa that are not highly represented at the Thomas Farm include urodeles, squamates, birds, and bats. Table II shows that specimens of several of these taxa are actually present in fairly large numbers, but their relative abundances are low when compared to the more numerous rodents and anurans. Among the hepatofauna, the urodele fauna consists of three species, with the salamandrid *Notophthalmus robustus* the most common. The aquatic salamander *Siren* is rare, and the large extinct *Batrachosauroides* is known from only a few specimens. Based on the life cycle of modern *Notophthalmus* in Florida (Ashton and Ashton, 1988; Franz, pers. comm., 1986), it is presumed that *Notophthalmus robustus* was entirely aquatic. The fairly low numbers of aquatic salamanders indicates that permanent water was not a characteristic of the site. The low representation of lizards and snakes in all layers is also notable. Snakes often appear to be underrepresented at fossil localities because large numbers of vertebrae are required to determine minimum numbers of individuals. Lizard remains are extremely delicate and may not have survived fossilization, or the low

numbers of lizards may indicate that these taxa were not common in the area.

Birds and bats each comprise less than 5% of the total numbers of individuals from any layer. The rarity of these volant taxa at fossil localities is usually attributed to their habitat preferences and the delicacy of their bones. Even though these taxa are relatively uncommon at Thomas Farm, the absolute number of specimens of these groups is high compared to other localities of similar age in Florida (Pratt, in prep.), and in fact, to other deposits in North America (Morgan, in prep.). The majority of bat taxa now known from the locality are most closely related to living species that are obligate cave dwellers (G. Morgan, pers. comm., 1986). This feature of the fauna indicates that bone and sediment deposition, particularly in the upper unit 15, was occurring in or near suitable chiropteran roosting sites such as caves. These caves may also have served as dens for mammalian carnivores or roosting sites of raptorial birds.

It is clear that the overall similarities in the types of vertebrates (by order) found in the various layers of the site (Table II) indicate a similarity in the habitat sampled throughout the course of deposition. The species recovered from the lower levels of the site and the upper levels are identical in terms of stage of evolution, so it is likely that deposition occurred over a relatively short time geologically.

Relative representation

Skeletal relative representation (Table VII) is a means of determining which elements have been lost from the complete skeleton following the death of the animal. By comparing skeletal percentage preservations of fossil remains with bone abundances in modern accumulations, it is possible to assess the similarity or difference between them, and to draw some conclusions as to the potential source of fossil bone.

Unit 15

As both fossil bone condition and faunal composition suggest that the majority of the

TABLE VII

Relative representations (Rel. rep.) of elements of *Proheteromys floridanus*, quartz grain equivalent ranks (dq_e), and transport groups (Trans grp). Actual quartz grain equivalents shown in Appendix I. See text for calculations of relative representations and quartz grain equivalents

Element	Rel. rep. (%)	dq_e rank	Trans. grp.		Element	Rel. rep. (%)	dq_e rank	Trans. grp.	
<i>Unit 15</i>					<i>Unit 6-7</i>				
Incisor	94.4	1	III	> 80%	Incisor	73.3	1	III	> 60%
Humerus	77.1	5	II/III		Tibia	30.0	3	III	
Cheekteeth	73.3	2	III		Cheekteeth	29.2	2	III	
Calc/astrag.	70.2	6	II/III	> 60%	Calc/astrag.	26.6	6	II/III	> 20%
Femur	53.8	4	II/III		Femur	16.7	4	II/III	
Ulna	50.3	11	I/II		Humerus	13.3	5	II/III	
Radius	48.1	8	II	> 40%	Ulna	13.3	11	I/II	
Tibia	39.2	3	III		Radius	6.7	8	II	
Dentary	36.0	10	II		Phalanges	5.5	14	I	
Pelvis	26.4	9	II		Metatarsal	4.6	13	I	
Metatarsal	25.0	13	I		Maxilla	3.3	7	II	
Maxilla	23.5	7	II		Scapula	3.3	12	I/II	
Phalanges	23.0	14	I		Dentary	3.3	10	II	> 0%
Scapula	20.7	12	I/II	> 20%	Pelvis	0	9	II	
Mean representation = 49.7%					Mean representation = 17.2%				
<i>Unit 11</i>					<i>Unit 5</i>				
Incisor	82.4	1	III	> 80%	Incisor	90.3	1	III	> 80%
Humerus	44.5	5	II/III	> 40%	Cheekteeth	30.9	2	III	
Calc/astrag.	39.4	6	II/III		Humerus	30.1	5	II/III	
Femur	36.9	4	II/III		Calc/astrag.	26.3	6	II/III	
Cheekteeth	35.8	2	II/III		Ulna	25.0	11	I/II	
Ulna	24.6	11	I/II		Tibia	22.2	3	III	> 20%
Tibia	21.6	3	III	> 20%	Pelvis	19.4	9	II	
Radius	19.2	8	II		Radius	16.7	8	II	
Pelvis	15.1	9	II		Femur	13.8	4	II/III	
Scapula	14.4	12	I/II		Metatarsal	12.2	13	I	
Metatarsal	11.9	13	I		Scapula	5.5	12	I/II	
Dentary	10.9	10	II		Phalanges	5.2	14	I	
Phalanges	5.7	14	I	> 0%	Dentary	2.8	10	I/II	> 0%
Maxilla	0	7	II		Maxilla	0	7	II	
Mean representation = 27.1%					Mean representation = 21.5%				

fossil remains from unit 15 form a coprocoenosis, relative representations of selected elements of the small heteromyid *Proheteromys floridanus* from the unit 15 sample were compared to modern scatological and pellet accumulations. Recent scat deposits were chosen for comparison based on the similarity (in size and morphology) of the mammalian carnivore that formed them, to Thomas Farm

canids. Relative representations of bones from scat of the coyote *Canis latrans* (Korth, 1979; Andrews and Nesbit Evans, 1983), the red fox *Vulpes vulpes* and the white-tailed mongoose *Ichneumia albicauda* (Andrew and Nesbit Evans, 1983) appear quite similar to relative representation values of fossil rodent elements (Fig. 5A-C). Statistical comparison of the relative representations of fossil elements with

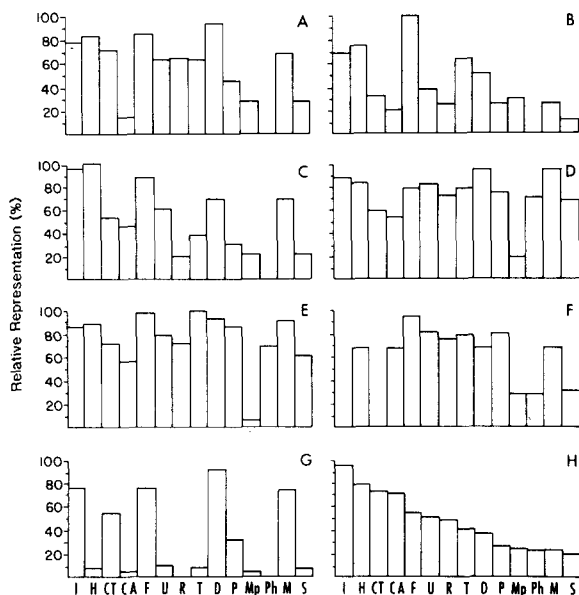


Fig. 5. Relative representations of selected skeletal elements from Recent mammalian carnivore scat, Recent avian raptor pellets, and from sediments at Thomas Farm. A. Coyote scat. B. Red fox scat. C. White-tail mongoose scat. D. Barn Owl pellets. E. Great-Horned Owl pellets. F. Screech Owl pellets. G. Red-Tailed Hawk pellets. H. Unit 15, Thomas Farm. Abbreviations: CA=calcaneum and astragalus; Ct=cheekteeth; D=dentary; F=femur; H=humerus; I=incisor; M=maxilla; Mp=metapodials; P=pelvis; Ph=phalanges; R=radius; S=scapula; U=ulna. Data for A from Korth (1979), for B-C from Andrews and Nesbit Evans (1983), for D-F from Dodson and Wexlar (1979).

relative representations of bones from Recent mammalian scat (Korth, 1979; Andrews and Nesbit Evans, 1983) shows that the relative representations of rodent elements from unit 15 are significantly different ($p \leq 0.01$) from those of Recent bone accumulations (Table VIIIA). This finding does not necessarily indicate that the Thomas Farm deposit of micromammals is not derived from a mammalian coprocoenosis, as the relative representations of bones from two different Recent coyote scat studies (Korth, 1979; Andrews and Nesbit Evans, 1983) are also significantly different from one another at the $P \leq 0.01$ level (Table VIIIA). This type of analysis is apparently too sensitive to individual and interspecific differences to be of use in differentiating coprocoenoses from other types of bone accumulations. On the basis of Spearman's coefficient of rank-order correlation, r_s (Sokal and Rohlf, 1981), which considers only the order of skeletal abundances, the unit 15 assemblage of small rodent elements possesses bone abundances similar to those found in scat of red fox and mongoose (Table IX). The rank abundances of small mammal bone in coyote scat do not appear similar to those of unit 15, unless calcanea, which have low representations in

TABLE VIII

Statistical comparison of bone relative representation values. Reported are calculated G values from the $R \times C$ test for association (Sokal and Rohlf, 1981, p. 599). Values greater than 27.68 indicate significant differences at $p \leq 0.01$ (d.f. = 13). Abbreviations: Cl(K), *Canis latrans* data from Korth (1979); Cl(A), *C. latrans* data from Andrews and Nesbit Evans (1983); Vv, *Vulpes vulpes*; Ia, *Ichneumia albicauda*, both from Andrews and Nesbit Evans, 1983; Ta, *Tyto alba*; Bv, *Bubo virginianus*; Oa, *Otus asio*; all from Dodson and Wexlar (1979); Bj, *Buteo jamaicensis*; from Pratt (1986)

Unit	Unit 15	Cl(K)	Cl(A)	Vv	Ia	Ta	Bv	Oa	Bj
A. Unit 15 Relative representations compared to Recent scat/pellet deposits									
15	—	59.8	529.8	73.1	59.8	103.2	95.9	40.3	341.2
Cl(K)	—	—	89.4	—	—	—	—	—	—
Unit	15	11	6–7	5					
B. Relative representations of heteromyid bones from Thomas Farm and rodent bones from Rodeo Ranch (RR); from Wolff, 1973 (n = 13)									
11	69.6	—							
6–7	81.0	75.6	—						
5	68.6	74.8	43.2						
RR	43.3	—	29.2						

TABLE IX

Spearman's coefficient of rank-order correlation, r_s , for relative representations of small mammal bones in fossil and Recent accumulations. Abbreviations: dq_e , quartz grain equivalent rank. For list of other abbreviations see Table VIII

Unit	n	Unit										
		15 14	Cl(K) 12	Cl(A) 14	\bar{V} 14	Ia 14	Ta 13	Bv 13	Oa 11	Bj 14	dq_e 14	RR 13
15	14		0.37	0.40	0.71**	0.62*	-0.11	0.27	0.61*	0.04	0.78**	0.71**
11	14	0.92**	0.11	0.24	0.62*	0.49	-0.30	0.15	0.61*	-0.10	0.73**	0.56*
6/7	14	0.78**	0.24	0.22	0.57*	0.35	-0.42	0.26	0.53	0	0.78**	0.78**
5	14	0.86**	0.10	0.07	0.44	0.33	-0.35	-0.02	0.49	-0.17	0.66*	0.59*

*Significant correlation at $P \leq 0.05$.

**Significant correlation at $P \leq 0.01$.

coyote feces (Korth, 1979; Andrews and Nesbit Evans, 1983) are eliminated from the analysis. If calcanea are not considered, rank abundances of elements from unit 15 are correlated with those from coyote scat ($r_s = 0.59$ for the Andrews and Nesbit Evans study, $r_s = 0.54$ for the Korth study).

Results of the tests discussed above suggest that the most reliable information can be gained by a careful examination of the patterns of similarity between fossil and recent bone accumulations. The relative representation value in a fossil element divided by its relative representation value in a Recent scatalogical accumulation provides an observed-to-expected ratio, shown in Table X. An observed/expected ratio of close to 1.0 indicates that the abundance of the fossil bone is similar to that in a modern comparative analogue, while values of greater or less than 1.0 indicate that differences in the abundance values exist that must be accounted for. Comparison of relative representations of *Proheteromys floridanus* elements from unit 15 with small mammal remains from scat of coyotes shows that the preservation values for fossil bones are more similar to those of bones from the coyote scat investigated by Korth (1979), with 50% of the fossil elements considered having relative representation ratios from 0.80 to 1.2 times those expected in coyote scat (Table XA). Comparison of the unit 15 assemblage with the coyote scat accumulation described by An-

drews and Nesbit Evans (1983), shows a higher representation of incisors, cheekteeth, tarsals, and phalanges in the Thomas Farm sample, and over 36% of the fossil elements have representations over 1.2 times greater than those seen in coyote scat (Table XB). Andrews and Nesbit Evans (1983) attribute the low representation of prey teeth in carnivore scat to mechanical destruction by chewing, although small bones (such as those of rodents) evidently are not as badly broken as are teeth of larger mammalian prey. However, digestibility of a bone has also been shown to be a function of its size. Skeletal remains of small mammals (less than 100 g) may suffer from 60 to 99% digestion, depending on the type of carnivore, the size of the prey, the amount of prey eaten, and the amount of fur ingested with the prey (Lockie, 1959; Floyd et al., 1978; Weaver and Hoffman, 1979; Meriwether and Johnson, 1980; Johnson and Aldred, 1982; Gamberg and Atkinson, 1988). The differences in the representation values of the two Recent studies may therefore be due in part to differences in sizes of the prey represented in each.

Relative representations of rodent bones from unit 15 are in 9 of 14 instances (65%) higher than those found in red fox scat (Table XC and Fig. 5B), indicating that a fox causes more bone destruction than the agent or agents responsible for formation of the fossil assemblage. Bones from scat of the white-tailed

TABLE X

Relative representations of skeletal elements of *Proheteromys floridanus* from unit 15 based on expected representations of elements from carnivore scat. For list of abbreviations see Table VII

Element	Rel. rep. ratio	dq_e rank	Trans. grp.		Element	Rel. rep. ratio	dq_e rank	Trans. grp.	
A. <i>Canis latrans</i> (Korth, 1979)					D. <i>Ichneumia albicauda</i> (Andrews and Nesbit Evans, 1983)				
Calc/astrag	3.69	6	II/III	> 1.00	Radius	2.64	8	II	
Humerus	1.11	5	II/III		Cheekteeth	1.41	2	I	
					Metatarsal	1.22	13	I	
Incisor	0.94	1	III		Calc/astrag	1.17	6	II/III	
Cheekteeth	0.92	2	III		Tibia	1.07	3	III	> 1.00
Radius	0.81	8	II		Incisor	0.98	1	III	
Tibia	0.81	3	III		Scapula	0.91	12	I/II	
Ulna	0.80	11	I/II		Phalanges	0.90	14	I	
Femur	0.77	4	II/III	> 0.50	Ulna	0.85	11	I/II	
Scapula	0.46	12	I/II		Pelvis	0.83	9	II	
Dentary	0.39	10	II		Humerus	0.77	5	II/III	
Maxilla	0.30	7	II		Femur	0.66	4	II/III	
Pelvis	0.21	9	II		Dentary	0.52	10	II	> 0.50
B. <i>C. latrans</i> (Andrews and Nesbit Evans)					Maxilla	0.36	7	II	
Calc/astrag	5.00	6	II/III		E. <i>Tyto alba</i> (Dodson and Wexlar, 1979)				
Cheekteeth	2.45	2	III		Calc/astrag	1.45	6	II/III	
Incisor	1.65	1	III		Cheekteeth	1.22	2	III	
Phalanges	1.47	14	I		Incisor	1.09	1	III	
Scapula	1.44	12	I/II	> 1.00	Phalanges	1.01	14	I	> 1.00
Metatarsal	0.97	13	I		Humerus	0.94	5	II/II	
Ulna	0.78	11	I/II		Femur	0.69	4	II/III	
Humerus	0.77	5	II/III		Radius	0.65	8	II	
Radius	0.67	8	II		Ulna	0.62	11	I/II	
Pelvis	0.63	9	II		Tibia	0.51	3	III	> 0.50
Femur	0.54	4	II/III	> 0.50	Dentary	0.39	10	II	
Tibia	0.46	3	III		Pelvis	0.35	9	II	
Maxilla	0.41	7	II		Scapula	0.27	12	I/II	
Dentary	0.38	10	II		Maxilla	0.25	7	II	
C. <i>Vulpes vulpes</i> (Andrews and Nesbit Evans, 1983)					F. <i>Bubo virginianus</i> (Dodson and Wexlar, 1979)				
Calc/astrag	3.74	6	II/III		Phalanges	1.25	14	I	
Cheekteeth	2.34	2	III		Calc/astrag	1.22	6	II/III	
Radius	1.92	8	II		Incisors	1.08	1	III	
Scapula	1.65	12	I/II		Cheekteeth	1.03	2	III	> 1.00
Ulna	1.34	11	II		Humerus	0.88	5	II/III	
Incisor	1.31	1	III		Radius	0.66	8	II	
Phalanges	1.15	14	I		Ulna	0.64	11	I/II	
Pelvis	1.06	9	II		Femur	0.56	4	II/III	
Humerus	1.02	5	II/III	> 1.00	Tibia	0.50	3	III	> 0.50
Maxilla	0.94	7	II		Dentary	0.39	10	II	
Metatarsal	0.87	13	I/II		Scapula	0.34	12	I/II	
Dentary	0.72	10	II		Pelvis	0.31	9	II	
Tibia	0.63	3	III		Maxilla	0.25	7	II	> 0.20
Femur	0.54	4	II/III	> 0.40					

TABLE X (continued)

Element	Rel. rep. ratio	dq _e rank	Trans. grp.		Element	Rel. rep. ratio	dq _e rank	Trans. grp.	
G. <i>Otus asio</i> (Dodson and Wexlar, 1979)					H. <i>Buteo jamaicensis</i> (Pratt, 1986)				
Humerus	1.15	5	II/III	> 1.00	Calc/astrag	46.34	6	II/III	
Calc/astrag	0.96	6	II/III		Metatarsal	20.15	13	I/II	
Incisor	0.92	1	III		Radius	*	8	II	> 10.00
Cheekteeth	0.91	2	III		Humerus	12.36	5	II/III	
Radius	0.64	8	II		Ulna	8.08	11	I/II	
Scapula	0.62	12	I/II		Tibia	4.17	3	III	
Ulna	0.61	11	I/II		Scapula	3.30	12	I/II	
Femur	0.56	5	II/III		Incisor	1.28	1	III	
Tibia	0.50	3	III	> 0.50	Cheekteeth	1.15	2	III	> 1.00
Dentary	0.42	10	II		Pelvis	0.84	9	II	
Maxilla	0.35	7	II		Femur	0.71	4	II/III	> 0.50
Pelvis	0.31	9	II		Dentary	0.38	10	II	
Phalanges	0.28	14	I		Maxilla	0.31	7	II	

*Denominator of 0.

mongoose are similar to those of unit 15 micromammal accumulation in terms of representation (Table XD, Fig.5C), with 50% of fossil to Recent bone relative representations falling between 0.80 and 1.2, although the majority of the prey species taken by this mongoose are larger than small rodent size (Andrews and Nesbit Evans, 1983).

Comparison of relative representations of heteromyid rodent bones from unit 15 with the range of relative representations from the scat of the mammalian predators discussed above shows that abundances of the majority (10 of 14) of fossil elements fall within the observed ranges of bone abundances from feces of Recent mammalian carnivores (Fig.6A). Andrews and Nesbit Evans (1983) caution that bone relative representations are not as reliable indicators of a fossil coprocoenosis as are bone surface features because other types of taphonomic factors can result in patterns of relative representations similar to those found in a scatological deposit. However, few taphonomic factors have been demonstrated to result in high levels of relative representation such as those seen in Recent scat or in the unit

15 assemblage. The hypothesis that the collection of *Proheteromys floridanus* bones in unit 15 represent a relatively unmodified coprocoenosis formed by a mammalian carnivore is therefore supported by the relative representation data.

Relative representations of small mammal bones obtained from pellets of Barn Owls or Great-Horned Owls (Fig.5D, E) are extremely high (Dodson and Wexlar, 1979; Korth, 1979, Pratt, 1979). Screech owls, Red-Tailed Hawks, and other hawks often break the bones of their prey (Clark, 1972; Pratt, 1979), with the result that preservation of prey bone is lower than that of the larger owls (Fig.5F, G). The extremely corrosive stomach acids of hawks causes complete destruction of some elements (Duke et al., 1975). My investigations of avian pellets show that because some elements ingested by hawks may be completely digested, the pattern of representation of elements in pellets cast by diurnal raptors is quite different from the representation of elements in owl pellets (Fig.5G).

Figure 6B and Table XE-H show that relative abundances of most rodent elements

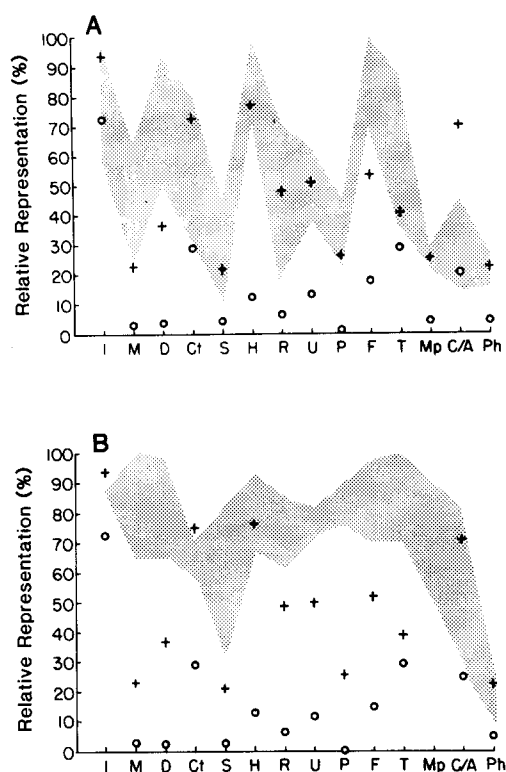


Fig.6. Ranges of relative representations of mammalian skeletal elements in scat of coyote, red fox, and mongoose, indicated by shaded area (data from Korth, 1979; Andrews and Nesbit Evans, 1983). B. Ranges of relative representations of mammalian skeletal elements in pellets of Barn Owl, Great-Horned Owl, and Screech Owl indicated by shaded area (data from Dodson and Wexlar, 1979). Relative representations of elements of *Proheteromys* elements from unit 15 indicated by +. Relative representations of *Proheteromys* elements from unit 6-7 indicated by o. For list of abbreviations see Fig.5.

from unit 15 are generally lower than those of bones derived from owl pellets. Relative representations of rodent bones in unit 15 and in all avian raptor pellets except for Screech Owls are also significantly different (Tables VIIIA and IX). The statistical results indicate that the likelihood of the unit 15 deposit representing an unmodified avian pellet deposit is fairly low. It is possible that the original accumulation in unit 15 was initially similar to that formed by a bird of prey such as an owl, but was subsequently modified by additional taphonomic factors such as weathering destruction or water-mediated transport. This hypothesis will be discussed below, although it

is not as strongly supported by the data as is a mammalian carnivore source for the bones.

Table XI lists relative representations of bufonid elements from unit 15, and Table XII lists the ratios of these values to *Osteopilus* (Hylidae) element preservation in Barn Owl pellets collected in the Cayman Islands (Morgan, 1977). The urostyle and ulna are more abundant in the fossil accumulation than in recent pellets, but the $R \times C$ test of association (Sokal and Rolf, 1981) indicates that relative representations of frog elements from unit 15 are not significantly different from those in the owl pellet accumulation ($G=13.4$ at 5 d.f.,

TABLE XI

Relative representations of anuran elements from Thomas Farm, quartz grain equivalent ranks, and transport groups. For list of abbreviations see Table VII

Element	Rel. rep. (%)	dq_e rank	Trans. grp.
A. Unit 15			
Ilium	91.4	2	III
Rad/ulna	89.7	3	III
Humerus	77.6	1	III
Urostyle	68.9	5	I/II
Sacrum	35.1	4	I/II
Scapula	32.2	6	I
B. Unit 11			
Rad/ulna	75.6	3	III
Ilium	75.0	2	III
Humerus	66.3	1	III
Urostyle	50.0	5	I/II
Scapula	30.4	6	I
Sacrum	32.7	4	I/II
C. Unit 6/7			
Ilium	83.3	2	III
Humerus	66.6	1	III
Urostyle	46.3	5	I/II
Rad/ulna	32.4	3	III
Sacrum	14.8	4	I/II
Scapula	14.8	6	I
D. Unit 5			
Ilium	90.1	2	III
Humerus	45.5	1	III
Urostyle	39.1	5	I/II
Rad/ulna	31.6	3	III
Scapula	19.4	4	I
Sacrum	18.4	6	I/II

TABLE XII

Preservation ratios of relative representations of bufonid elements from unit 15 of Thomas Farm to representations of anuran elements from Barn Owl pellets from the Cayman Islands. For list of abbreviations see Table VII

Element	Rel. rep. ratio	dq_e rank	Trans. grp.
Rad/ulna	2.43	3	III
Urostyle	1.84	5	I/II
Scapula	1.35	6	I
Humerus	1.17	1	III
Sacrum	1.17	4	I/II
Ilium	0.95	2	III

$P \leq 0.01$). A relative representation pattern similar to that found in an owl pellet accumulation supports the view that a predator of some type may have been responsible for deposition of the majority of bufonid remains.

The overall similarities of unit 15 microfaunal bone abundances and those in mammalian scat suggest that the rodent and bufonid elements in this layer may have been deposited by one or more predatory species. Alternatively, the original coprocoenosis may have initially possessed high abundances of most bone types and was subsequently modified by other taphonomic factors. The possibility that the deposit resembles but does not actually represent a coprocoenosis, but was formed by some other means, must also be investigated.

Although relative representations of *Proheteromys* elements from unit 15 are significantly different from prey bone abundances in selected mammalian carnivore scat (Table VIIIA), when compared to the range of skeletal abundances in mammal scat (Fig. 6A), there is no discernable grouping of fossil bones having lower than expected preservations. Representations of most elements are similar to the general mammalian carnivore pattern. Therefore if the hypothesis that the unit 15 assemblage represents, at least in part, a mammalian carnivore fecal deposit, it seems likely that the bones were buried fairly rapidly, before major

effects of water transport or weathering caused modification of the original deposit. However, nearly all fossil bone relative representations are lower than bone representations in owl pellet accumulations (Fig. 6B). With the exception of the phalanges (Table XE-H), the best represented elements in unit 15 are those with the largest quartz grain equivalents, members of lag groups III and II/III. The tibia, which also belongs in this group, has a much lower representation. Elements having lowest observed-to-expected representations belong in the less dense, more easily transported category. The high representation of phalanges and the relatively low representation of the tibia are not consistent with an interpretation of the fossil assemblage representing a deposit composed of complete or nearly complete skeletons, such as an accumulation formed by owls, that was further modified by the effects of fluvial sorting.

If the concentration of microvertebrate remains in unit 15 was formed either solely or primarily by the action of moving water, then actual relative representation values (Table VII) should indicate groups of elements that either were transported together, or resisted transport. In fact, the order of abundances from highest representation to lowest is not significantly different from predicted order of abundance based on quartz grain equivalent rank from largest to smallest, a representation pattern expected in a fluvial lag deposit (Table IX). Relative representation rankings are also not significantly different from abundance ranks of bones from the Rodeo Ranch locality (Wolff, 1973). However, other evidence such as overall high relative representation and lack of water-worn elements in unit 15 suggests that fluvial sorting was not a major factor in this level. The similarity of bone abundances to those in a hypothetical fluvial lag deposit probably reflects the fact that the most dense elements, in addition to resisting transport in moving water, are also less affected by other taphonomic factors such as breakage, digestion, and weathering (Winkler, 1983). For this reason, in nearly any type of

microvertebrate deposit the most common elements may well be those that are the most sturdy (Andrews and Nesbit Evans, 1983).

Relative representation of bufonid elements from unit 15 compared with their respective quartz grain equivalent ranks are shown in Table XI. Although the most highly represented elements, the ilium and ulna, are similar in settling velocity and hence in equivalent quartz grain diameter, the high representation of other elements possessing a range of equivalent quartz grain sizes supports the conclusion based on the rodent data that unit 15 was not greatly affected by selective transport.

The features of the concentration of microvertebrate bones in unit 15 points strongly to the conclusion that this level contains a mammalian or avian predator coprocoenosis (or some combination of the two, but with a stronger mammalian component). It appears that the original assemblage was somewhat (but not greatly) modified either by transport in running water or by climatic effects. If unit 15 relative representations of rodent elements are compared statistically with those of the lower sedimentary layers, they are all significantly different (Table VIII B). However, the rank of bone abundances is similar in all layers examined, as shown by the Spearman coefficient of rank-order correlation (Table IX). The similarity of order of abundances suggests that the original source of the rodent elements may have been a coprocoenosis, but the lower mean representations (Table VII) indicates that additional taphonomic factors played a role in the formation of the lower sedimentary layers of Thomas Farm.

Unit 11

Relative representations of elements compared with their quartz grain equivalents shows that the most highly represented elements in unit 11 (greater than 35% preservation) have large equivalent grain sizes (Table VII). For the most part (with the exception of the tibia, which should be in this group), the most abundant bones are lag elements (Trans-

port Group III), suggesting that running water may have had sufficient power to winnow out many of the lighter, more readily transported elements. The most highly represented anuran elements also have relatively large equivalent quartz grain sizes (Table XI).

Unit 6-7

Unit 6-7 rodent remains have the lowest mean percentage preservation value (17.5%), indicating that even if microvertebrate elements in this layer were deposited by a carnivore, other taphonomic factors have completely obscured the original bone source (Fig. 6A). All elements except the incisor and calcaneum are less abundant in unit 6-7 than they are in either mammalian or avian scat/pellet accumulations. The Spearman coefficient of rank-order correlation (Table IX) shows that the order of element representation in this unit is extremely similar to rodent bone representation in the Rodeo Ranch fluvial deposit (Wolff, 1973). It seems very likely that the microvertebrate remains in unit 6-7, regardless of their original source, were affected by a water current strong enough to cause selective sorting of the elements.

Unit 5

The mean preservation value of elements in unit 5 is slightly higher than that of unit 6-7 (21.5%), but is too low to indicate an unmodified coprocoenosis. Although bone abundances in this unit are significantly different from those in unit 6-7 (Table VIII) these two levels are by far the most similar in terms of rodent element relative representation. Other evidence has previously established that layers 6-7, and especially unit 5 were probably deposited under aquatic conditions (Pratt, 1986; in press), so evidence of modification by moving water is not surprising.

The similarities of the bone abundances in the lower layers to those of a water-sorted assemblage and their lack of similarity to an unmodified coprocoenosis (Table IX) suggest that moving water was present at the time of deposition of the sediments containing these

bones. An estimate of the speed of the current can be determined from the size of the quartz grain equivalents of the most well-represented elements, which in all 3 of the lower units are rodent incisors. The representation of this element is high (over 70% in all layers), so it may be assumed that for the most part current speeds were not sufficient to cause its removal from the site of deposition. Reference to the predicted current velocity graph based on transport of quartz grains (Allen, 1965; Behrensmeier, 1975) indicates that current speeds of over 35 cm/s would be sufficient to transport this element. Therefore it would appear that the current in the sink seldom exceeded 30–35 cm/s. This finding agrees well with the proposed current speed based on the megafaunal analysis (Pratt, 1986; in press).

Summary

Evidence suggests that the microvertebrate component of the Thomas Farm fauna was derived predominantly from a coprocoenosis, but that some of the less common remains (bats, lizards, birds) were deposited attritionally. The uppermost sand unit 15, characterized by the greatest abundance of microfauna, represents at least in part a relatively unmodified coprocoenosis, deposited in or near a limestone cave. Based on bone breakage patterns and evidence of bone digestion, high mean relative representation of elements, and the predominance of two microvertebrate taxa (*Proheteromys floridanus* and *Bufo praeivius*), the most likely source of the bones was one or more fox-to coyote-sized mammalian predators.

The lower sand and clay units are somewhat different from the uppermost layer in possession of a higher proportion of aquatic forms, low overall preservation of microvertebrate remains, and bone preservation patterns similar to those seen in assemblages modified by moving water (Wolff, 1973). The rodent and toad elements present in these layers may have washed into a water-filled sinkhole from a local scat accumulation, and were further modified by the effects of moving water within the sink,

although the current apparently was not strong or persistent. This interpretation is supported by analysis of the megafauna, as aquatic forms are most numerous in units 5 and 6–7, and larger bones show significant patterns of long axis orientation indicative of those produced by moving water (Pratt, 1986; in press). The faunal composition and relative abundances of vertebrates found within the various sedimentary layers indicate that the fauna sampled, local habitat and environment all must have been relatively constant throughout the entire cycle of sinkhole deposition. Therefore although different taphonomic factors were acting to varying degrees in the modification of the bone deposits from the different levels of the site, the time sampled was probably relatively short.

Conclusions

The Thomas Farm locality sampled a relatively autochthonous fauna of microvertebrates living in close proximity to a sinkhole–cave complex. Diversity and equitability of rodent taxa is low, probably due to a taphonomic bias toward one species of heteromyid rodent. Several other recently discovered (but as yet undescribed) early Miocene microvertebrate localities in Florida contain a higher diversity of rodents than does Thomas Farm; however, members of the genus *Proheteromys* appear to have been the dominant rodents in Florida during the early Miocene. *Proheteromys floridanus* was a brachydont, quadrupedal form and probably frequented forested areas (Pratt, 1986). The presence of arboreal and scansorial sciurids (Pratt and Morgan, 1989), as well as several species of hylid tree frogs, also provide evidence that the region surrounding the sinkhole may have been wooded. The presence of bats indicates that caves occurred in the vicinity of the sinkhole, particularly during the final stages of filling of the sink.

The small ranid frog and aquatic salamander found in the lower units of the site indicate that the sinkhole contained water on at least a

seasonal basis. However, the lack of fish and the relative rarity of larger aquatic forms such as turtles and alligators (Pratt, 1986; in press) suggest that drainage was relatively restricted, and that the sinkhole was not connected to a stream or river.

Little is known about the climate of Florida in the early Miocene. Floral evidence from the early Miocene of the Florida panhandle (Berry, 1916) indicates that conditions may have been more tropical than those in north Florida today.

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Appendix I — Settling velocities, quartz grain equivalents and ranks for skeletal elements of *Peromyscus* and *Rana*. See text for explanation.

Element	Settling velocity (cm/sec)	dq_e (mm)	dq_e rank	Trans. grp.
<i>A. Peromyscus</i>				
Incisor	10.89	1.10	1	III
Cheektooth	9.96	0.87	2	III
Tibia/fibula (dist.)	8.70	0.70	3	III
Femur (prox.)	7.96	0.59	4	II/III
Humerus (dist.)	7.63	0.54	5	II/III

Element	Settling velocity (cm/sec)	dq_e (mm)	dq_e rank	Trans. grp.
Calcaneum/astragalus	7.10	0.47	6	II/III
Maxilla (edent.)	6.87	0.44	7	II
Radius (prox.)	6.56	0.40	8	II
Ilium/acetabulum	6.54	0.39	9	II
Dentary (edent.)	6.36	0.38	10	II
Ulna (prox.)	5.78	0.31	11	I/II
Scapula (prox.)	5.41	0.27	12	I/II
Metatarsal	4.93	0.23	13	I
Phalanges	4.00	0.15	14	I
<i>B. Rana</i>				
Humerus	16.58	2.55	1	III
Ilium	10.51	1.04	2	III
Radius/ulna	8.78	0.70	3	III
Sacrum	5.8	0.32	4	I/II
Urostyle	5.69	0.30	5	I/II
Scapula	4.88	0.22	6	I

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