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ABSTRACT

The Leisey Shell Pit in southwestern Hillsborough County, Florida, contains several lenses rich in vertebrate fossils within a thick bed of marine shells referable to the Bermont Formation. The largest concentration of vertebrate remains (Leisey 1A) was found in a 5 to 30 cm thick layer that extended over an area of about 2000 m^2. About 120 vertebrate taxa have been recovered from Leisey, representing nearshore marine, estuarine, freshwater, and terrestrial habitats. The terrestrial fauna is dominated by large mammalian herbivores, most notably *Glossotherium*, *Nothrotheriops*, *Equus*, *Tapirus*, *Palaeolama*, *Hemiauchenia*, *Platygonus*, and *Mammuthus*. Carnivores, including *Canis edwardii*, *Smilodon gracilis*, and *Arctodus pristinus*, and medium-sized herbivores, e.g. *Odocoileus*, *Mylohyus*, and *Sylvilagus* are much less common. Small mammals are rare at Leisey 1A, but more abundant at other Leisey sites, notably Leisey 3A. Leisey 3A also preserves a large sample of *Hemiauchenia macrocephala*, probably a catastrophic assemblage of a single herd. The stage of evolution of the species of *Holmesina*, *Sigmodon*, *Smilodon*, *Canis*, *Tapirus*, *Platygonus*, *Palaeolama*, and *Mammuthus* indicates a late early Irvingtonian (early Pleistocene) age, about 1.5 to 1.0 Ma. Gar, tortoises (*Geochelone*), emydid turtles, *Alligator*, and birds are also well represented. Preliminary paleoecologic studies indicate a complex taphonomic history for the region. The most important features of the Leisey fauna are: 1) its large sample sizes of the dominant herbivores; 2) the appearance of taxa previously unknown or very poorly known from Florida (e.g. *Nothrotheriops* and a miniature glyptodont); and 3) the potential for correlation between marine and terrestrial biochronologies.

INTRODUCTION AND HISTORY OF INVESTIGATIONS

Along the southwestern coast of peninsular Florida are numerous small quarries or shell pits, from which each year thousands of tons of shells and sand are mined for use in road construction. Terrestrial vertebrate fossils are occasionally recovered from these quarries, scattered in among millions of mollusk shells. Previously, vertebrate fossils were only very rarely known to occur in concentrations sufficient to warrant serious excavation by paleontologists. In July of 1983, dragline operators at the Leisey Shell Pit, located 6.7 km (4 mi) southwest of Ruskin in southwestern Hillsborough County (W1/2 Sec. 15, T32S, R18E, Ruskin Quadrangle, USGS 7.5 minute series; 27° 42' N, 82° 30' W; Figs. 1 & 2), uncovered a very rich layer of vertebrate fossils. Frank Garcia, an experienced fossil collector, recognized the importance of the discovery and convinced the quarry owners to change their digging plans and temporarily preserve the site. During the remainder of 1983, Garcia, Ron Shrader, and others excavated an area of about 700 m^2. Garcia and Shrader subsequently donated much of the fossil material they recovered in 1983 (several thousand catalogued specimens) to the Florida Museum of Natural History (formerly the Florida State Museum). After a three month hiatus, the site was reopened in April 1984 as a cooperative effort of the museum, the Tampa Bay Mineral and Science Club, and Leisey Shell Pit, Inc., the owners of the property. Excavations were halted in September 1984 after an additional 1300 m^2 had been dug. All fossils recovered in 1984 are currently housed in the Vertebrate Paleontology Collection of the Florida Museum of Natural History. The site excavated in 1983-1984 is without exception the richest (both in terms of numbers of species and individuals) early Pleistocene megavertebrate assemblage in the southeastern

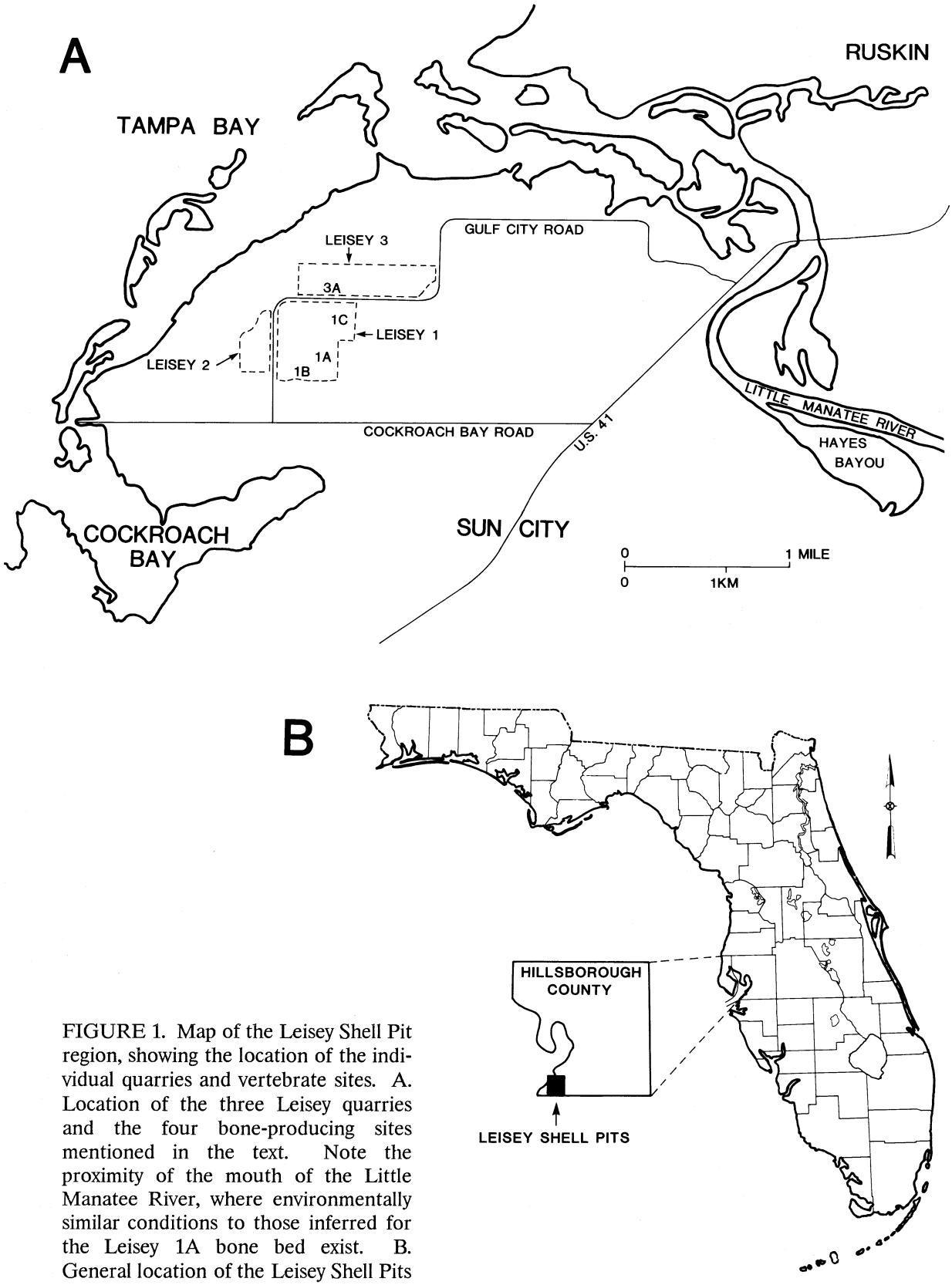

FIGURE 1. Map of the Leisey Shell Pit region, showing the location of the individual quarries and vertebrate sites. A. Location of the three Leisey quarries and the four bone-producing sites mentioned in the text. Note the proximity of the mouth of the Little Manatee River, where environmentally similar conditions to those inferred for the Leisey 1A bone bed exist. B. General location of the Leisey Shell Pits in Hillsborough County.

United States, and one of the richest in North America. It is, however, by no means the only significant concentration of fossil vertebrates to be recovered at Leisey.

In cases like this, the Florida Museum of Natural History uses a code to identify each particular site or fossil-bearing horizon within a quarry. Each quarry is assigned a number, and each site within a quarry a letter. The combination "Leisey Shell Pit 1A" (shortened to Leisey 1A) serves to specify only those specimens recovered from the main 1983-1984 site. Specimens not collected at designated sites are only assigned a quarry number, but not a letter (e.g., Leisey 2). By 1988, there were three numbered Leisey quarries and five lettered sites (Leisey 1A, 1B, 1C, 3A, and 3B; see Fig. 1). Leisey 1B was actually discovered by Frank Garcia before he found Leisey 1A, but it could not be extensively excavated without undercutting a road necessary for the mining operations of the quarry. It was finally excavated by Garcia and the Tampa Bay Mineral and Science Club in 1985 and 1986. The Florida Museum of Natural History has a small but synoptic collection of the vertebrates recovered from Leisey 1B. Leisey 1C refers to a small collection of vertebrate fossils recovered from a thin zone on top of the Hawthorn Group at the north end of quarry 1 (Fig. 1). Unlike the other sites discussed here, Leisey 1C is not Pleistocene, but late Miocene, and represents the remnants of a once more extensive stratum of the Bone Valley Formation. Elsewhere in the quarry, Pleistocene deposits rest directly on middle Miocene sediments, and all traces of a late Miocene stratum were eroded away. Leisey 2 was in fact the first Leisey quarry to be mined (Fig. 2A). Leisey 2 specimens were obtained by the Florida Museum of Natural History through donations by James Ranson and Eric Fernandez. No in situ concentrations of vertebrates are known from Leisey 2. Leisey 3A (Fig. 1) was found by Frank Garcia in November of 1986, and dug from December 1986 through February 1987. Leisey 3A is the second richest of the known Leisey sites, and in many ways complements that of Leisey 1A. Leisey 3B was discovered in December of 1987 by a museum field crew led by David Webb and Gary Morgan. It lies close to but stratigraphically well below Leisey 3A, and was found only when the water level in the quarry dropped about a meter to reveal a dark, organic layer. This stratum is apparently extensive throughout Leisey 3, but has not yet been systematically collected. In the accounts that follow, primary attention will be given to Leisey 1A, because it is the most thoroughly studied and productive site.

STRATIGRAPHY

The general stratigraphy of the Leisey quarries (Fig. 3) consists of massive, nearshore marine shell beds unconformably overlying an indurated bedrock of phosphatic, tan to light gray dolostone tentatively referred to the Hawthorn Group of Scott (1988). Shells of invertebrates are absent in the Hawthorn at Leisey, and vertebrate remains consist mostly of waterworn fragments of sirenian and cetacean bones, and shark teeth. A single lower molar of a primitive merychippine-grade horse (UF 53819), indicative of a late Hemingfordian or early Barstovian age (early middle Miocene, about 16 Ma [Mega-anna, millions of years ago]), was collected from the Hawthorn Group at Leisey. It matches identically merychippine teeth recently recovered from the Hawthorn at Nichols Mine in Polk County, about 35 km east-northeast of Leisey. The shell beds are in turn overlain by massive, unconsolidated, and generally unfossiliferous beds of Quaternary quartz sand (Fig. 3).

The units at Leisey bounded by the Hawthorn Group below and the quartz sand above (Fig. 3) form about an 8 m thick sequence of alternating poorly consolidated, sandy, marine shell beds and laterally discontinuous, thin, freshwater marls. The combined Leisey Shell Pit invertebrate fauna is composed of over 200 species (mostly living species of bivalves and gastropods) with *Chione cancellata* especially abundant (Morgan et al., in prep.). Two faunal assemblages of mollusks are recognized at Leisey: an older unit ("lower shell bed") with about 10% extinct species, and a younger zone ("upper shell bed") with less than 5% extinct species. The former is compositionally most similar to faunas collected from the type region of the Bermont Formation along Shell Creek in Charlotte County, Florida and from the Belle Glade Rock Pit, Palm Beach County. Especially diagnostic is the presence of *Miltha carmenae*, *Fasciolaria okeechobensis*, and *Strombus mayacensis*. The lithologically similar Caloosahatchee Formation contains many more extinct species (50 to 65%, DuBar, 1958; Stanley, 1986). The upper shell bed contains a much lower diversity of mollusks than the lower, 93 species to 145 (Morgan et al., in prep.), and has almost no extinct species. These differences might result from either a more restricted environment, or from a

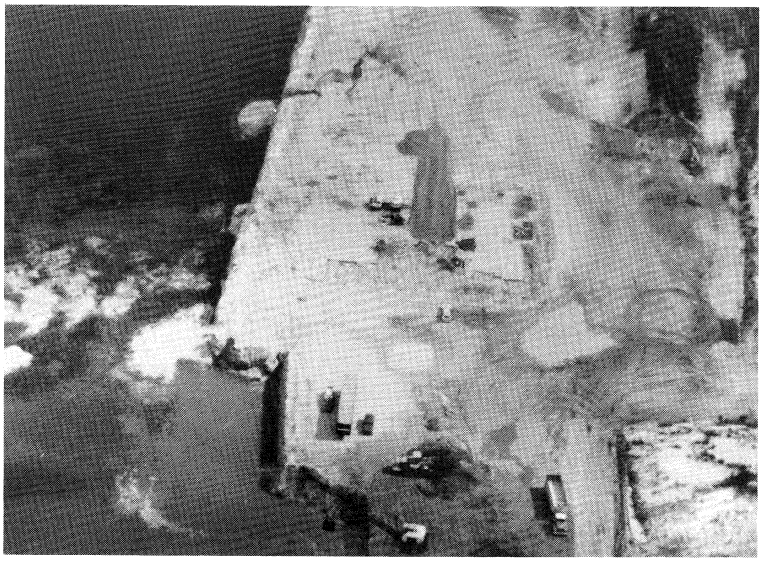

FIGURE 2. Air photos of Leisey Shell Pit 1A during excavations in June, 1984. A. Oblique view looking to the west-southwest. The road in the background is the north-south portion of Gulf City Road, and the water-filled quarry to the west of the road is Leisey 2. Leisey 1A is located directly to the right (north) of the dragline and the trailer. B. View of the site from the south, looking almost due north. The dark strip is an area where overburden has been freshly cleared by a bulldozer. The white objects in the site are plaster jackets of proboscidean remains.

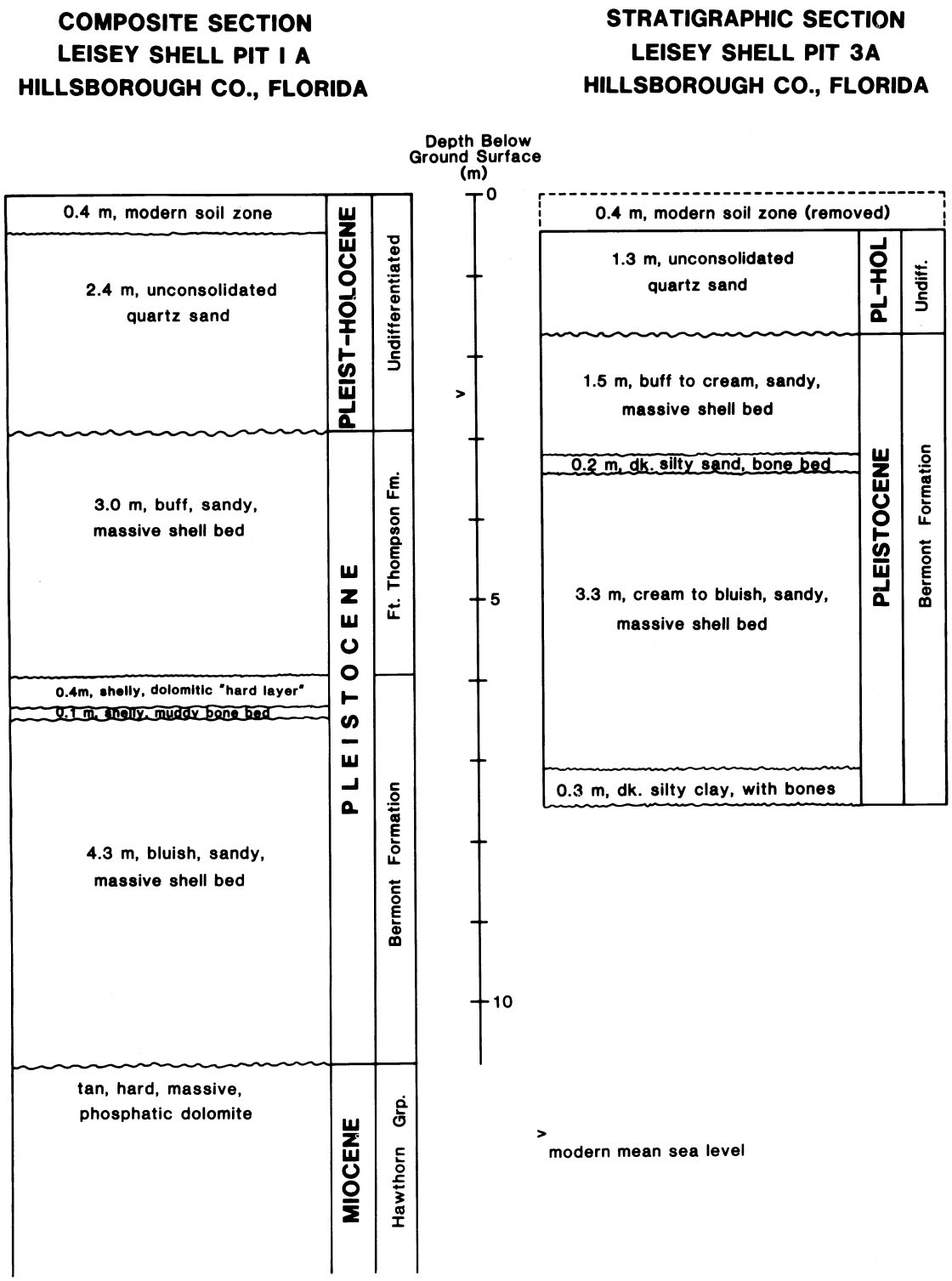

FIGURE 3. Composite geologic section of the Leisey Shell Pit, southwestern Hillsborough County, Florida, measured by the authors in 1984 and 1986. See text for details.

substantial difference in age (or both). The upper shell bed is tentatively assigned to the Fort Thompson Formation, which is characterized by having less than 5% extinct species. It should be noted that there are few or no valid lithologic criteria for distinguishing the Caloosahatchee, Bermont, and Fort Thompson formations, only the differing composition of their molluscan faunas. The stratigraphic code necessitates lithologic differences for recognition of lithostratigraphic units, but we employ these terms based on their widespread use in the geologic literature of southern Florida. In the northern half of the Leisey quarries the upper shell bed is often absent, and Quaternary alluvium rests directly on the Bermont Formation (Fig. 3).

The lower shell bed also differs from the upper bed by the presence of lenses of vertebrate-bearing sediments. The sedimentary composition of these lenses varies (reflecting slightly different depositional environments), but they usually contain a substantial fraction of organic-rich silt and mud, giving them a darker appearance than the surrounding shells and sand. The best studied of these lenses is the Leisey 1A bone-bed, which forms a well defined 5 to 30 cm thick layer. Its lithology comprises an unconsolidated, poorly sorted mixture of marine and freshwater mollusk shells, bones (including both complete elements and a large proportion of broken fragments), mangrove roots, palm seeds, fine-grained sand, silt, and dark brown mud. The areal extent of Leisey 1A is about 2000 m^2. It gradually pinches out laterally, with the vertebrate remains becoming increasingly scarce towards the margins of the bed. The taxonomic composition of the marine mollusks from Leisey 1A is similar to that from the lower shell bed, with some differences in relative abundances, but differs drastically in the large numbers of freshwater gastropods. Immediately above the bone bed, and separated from it by a poorly defined unconformity, was a 30 to 50 cm thick layer of indurated calcareous marl. This "hard layer" contained abundant freshwater gastropods (especially *Planorbella scalaris*), some marine mollusks (many of which were fragmented and apparently reworked), fine-grained sand, and occasional bones, almost exclusively of freshwater taxa such as turtles, *Alligator*, ducks, wading birds, and fish. Well defined erosional unconformities above the "hard layer" and below the bone bed separate them from the marine shell beds (Fig. 3).

Although of approximately similar age and containing essentially the same vertebrate fauna, Leisey 3A and Leisey 3B differ from Leisey 1A in several respects. Leisey 3A lacks mangrove roots, palm seeds, and the overlying marl layer. Its areal extent is about one quarter of Leisey 1A's, and also differs by being overlain by the Bermont Formation rather than the Fort Thompson. Leisey 3B differs from both Leisey 1A and Leisey 3A in lacking marine mollusk shells, consisting primarily of a layer of dark organic matter, silt, and mud that varies laterally in thickness from 20 cm to greater than 1.0 m. Mollusks are limited to freshwater species. It also lacks the mangrove roots, palm seeds, and the overlying marl layer of Leisey 1A, but contains a significant sample of as yet unidentified, carbonized wood and locally abundant *Alligator* coprolites. Leisey 3B represents a very widespread stratum through quarry 3, but vertebrate remains are typically rare and scattered, and as of May 1989 never concentrated to the degree of Leisey 1A or 3A.

VERTEBRATE PALEONTOLOGY

To date six classes and about 120 species of vertebrates have been identified from the Leisey Shell Pit local fauna (Tables 1 and 2), excluding the Miocene vertebrates. A sizable fraction of the material has not yet been sorted or intensively studied, so some additions to the fauna or changes in identification (especially at the species level) are anticipated. The following is a brief description of the vertebrate fauna, with some of the outstanding features highlighted. The entire fauna is being studied by various specialists, who will contribute to a forthcoming volume devoted to the Leisey fauna.

CHONDRICHTHYES.-- Ten species of sharks have been identified, along with two rays and a sawfish (Table 1). All but two of the sharks are referred to extant species that today are found in nearshore, shallow marine and estuarine environments. Leisey records one of the youngest well documented occurrences of the extinct snaggletoothed shark, *Hemipristis serra*, and the extinct mako shark, *Isurus hastalis*. The bull shark, *Carcharhinus leucas*, is the most abundant shark at Leisey and commonly enters modern shallow bays, estuaries, and rivers (Loftus and Kushlan, 1987).

TABLE 1. Preliminary faunal list of the sharks, rays, bony fish, amphibians, and reptiles from the Leisey Shell Pit 1A site, early Pleistocene (late early Irvingtonian), southwestern Hillsborough County, Florida. The lower vertebrates from the other Leisey sites have not yet been thoroughly studied.

Class Chondrichthyes
- Order Selachii
  - *Isurus hastalis*
  - *Carcharodon carcharias*
  - *Carcharhinus leucas*
  - *Carcharhinus* small sp.
  - *Hemipristis serra*
  - *Galeocerdo cuvieri*
  - *Negaprion brevirostris*
  - *Rhizoprionodon terraenovae*
  - *Ginglymostoma cirratum*
  - *Odontaspis taurus*
- Order Batoidea
  - *Pristis* sp.
  - *Dasyatis* sp.
  - *Myliobatis* sp.

Class Osteichthyes
- Order Semionotiformes
  - *Atractosteus spatula*
  - *Lepisosteus* sp.
- Order Siluriformes
  - *Ictalurus* sp.
- Order Perciformes
  - *Lepomis* sp.
  - *Centropomus* sp.
  - *Archosargus* sp.
  - *Lagodon rhomboides*
  - *Pogonias cromis*
  - *Sphyraena barracuda*
  - *Caranx hippos*
  - *Mugil* sp.
  - Labridae (gen. indet.)
- Order Elopiformes
  - *Megalops atlanticus*
- Order Tetraodontiformes
  - *Balistes* sp.
  - *Diodon* sp.

Class Amphibia
- Order Anura
  - cf. *Rana* sp.
  - *Bufo terrestris*
- Order Urodela
  - *Siren* sp.

Class Reptilia
- Order Testudines
  - *Macroclemys temmincki*
  - *Kinosternon* sp.
  - *Apalone ferox*
  - *Geochelone crassiscutata*
  - *Geochelone incisa*-group
  - *Gopherus polyphemus*
  - *Trachemys scripta*
  - *Terrapene carolina*
  - Cheloniidae (gen. indet.)[1]
- Order Squamata, Suborder Serpentes
  - *Nerodia* sp.
  - *Elaphe* sp.
  - cf. *Coluber* sp.
  - *Agkistrodon piscivorous*
  - *Crotalus adamanteus*
- Order Crocodilia
  - *Alligator mississipiensis*

[1]Presence based on a single hypoplastron from the hard marl layer above the bone bed.

OSTEICHTHYES.-- Fifteen taxa of bony fish are currently recognized from Leisey 1A (Table 1), but this number will undoubtedly increase as the material is properly analyzed, and the other sites are studied. Most of these, and all of the more common taxa are nearshore marine or estuarine species. Gar, especially the alligator gar, *Atractosteus spatula*, is the numerically predominant fish taxon, followed by the snook,

Centropomus. Gar scales were the most commonly found recognizable vertebrate remains at Leisey 1A, as several hundred could easily be recovered from a 5 m^2 area. Scales, of course, overestimate the abundance of the taxon, as each individual has so many. In any given area, gar vertebrae accounted for about half of the total number of fish vertebrae; this gives a more accurate representation of their relative abundance than do the scales. *A. spatula* today lives in nearshore marine, brackish and freshwater habitats along the western Gulf Coast, as far east as Choctawhatchee Bay, but no longer occurs in peninsular Florida (Wiley, 1976). At Leisey 3A, the sunfish *Lepomis* is the most common fish, and *Lepisosteus* is the more common gar.

AMPHIBIA AND REPTILIA.--Amphibians were extremely rare at Leisey 1A and were represented by only three taxa, the aquatic salamander *Siren*, a ranid frog, and a toad. They were much more common at Leisey 3A. Reptiles were abundant at all sites (Table 1), notably tortoises (two species of *Geochelone*), freshwater turtles (especially *Trachemys* and *Apalone*), and *Alligator*. Use of *Trachemys* as the genus name for the *scripta*-group of emydid turtles (instead of *Pseudemys*) follows the recent revision of Seidel and Smith (1986). Use of *Apalone* as the genus name for North American soft-shelled turtles (instead of *Trionyx*) follows the recent revision of Meylan (1987). Auffenberg (1988) described a new species of small tortoise from the late Irvingtonian Coleman 2A site, *Geochelone mlynarskii*, and limited the range of *G. incisa* to the Rancholabrean. The specific status of the small tortoise from Leisey 1A, certainly a member of the *G. incisa*-group, is under study by Peter Meylan, along with the remainder of the herpetofauna. Most of the turtle remains consisted of isolated shell elements. However, it was not uncommon to find elements of the same individual scattered over an area of 25 m^2 or less (a similar situation exists for the terrestrial mammals). Altogether, the remains of over 100 individual turtles were recovered from Leisey 1A alone. Also present were at least five species of snakes.

AVES.-- The very diverse Leisey avifauna consists of more than 30 species (several of which are new) represented by over 200 specimens and is under study by Steve Emslie, formerly of the Department of Zoology, University of Florida. Aquatic species, such as ducks, grebes and wading birds, are the most diverse and abundant taxa (Emslie, 1988). Perhaps the most spectacular avian fossils from Leisey are six elements (including most of a skull) of a new species of condor, *Gymnogyps kofordi*, that were donated to the museum by Frank Garcia, Don Ward, and Jim Pendergraft (Emslie, 1988).

MAMMALIA.--The mammals from the various Leisey Shell Pit localities are listed in Table 2. The fauna from Leisey 1A, although diverse, is lacking some important groups and underrepresented in others that are known to have been present and abundant in Florida during the early Pleistocene. These are predominantly medium to small-sized taxa such as shrews, moles, bats, rodents, and small carnivores. Several tons of matrix from Leisey 1A were washed to recover small vertebrates, but with very limited results with regards to mammals. Their rarity almost certainly reflects a taphonomic bias rather than a true indication of their representation in the original fauna. Large herbivores numerically dominate the Leisey 1A mammalian fauna, especially the llamas (*Palaeolama* and *Hemiauchenia*) and horses (represented by three species of *Equus*). Their combined minimum number of individuals (based on mandibles) exceeds 200 at Leisey 1A. Leisey 3A differed in that most of the large mammals (>90%) were of a single species, the long-legged camel *Hemiauchenia*, and it also had proportionally many more small mammals, especially the extinct cotton rat *Sigmodon libitinus*.

Two ground sloths were very common at Leisey 1A, *Glossotherium* and *Nothrotheriops*. Although two other sloth genera (*Megalonyx* and *Eremotherium*) are typically recovered from early Pleistocene sites in Florida (Kurtén and Anderson, 1980; McDonald, 1977), no material referable to them was recovered from Leisey 1A or Leisey 3A. Isolated specimens of *Eremotherium* have been found in the lower shell bed at Leisey 1 and 3. Both *Glossotherium* and *Nothrotheriops* are well represented by several nearly complete skulls, mandibles, isolated teeth, and numerous post-cranial elements. The presence of *Nothrotheriops* in Florida has previously been noted only from the Irvingtonian Pool Branch Site based on a few elements (McDonald, 1985; not Coleman 2A as stated by Webb and Wilkins, 1984). The large sample from Leisey confirms the presence of *Nothrotheriops* in Florida during the early Pleistocene, but this small ground sloth is unknown from the Rancholabrean of eastern North America. Except for being slightly smaller in size, the Leisey sample morphologically resembles late Pleistocene *Nothrotheriops shastensis* from the southwestern United States. Likewise, the Leisey specimens of *Glossotherium* are smaller than average *G. harlani* from the Rancholabrean.

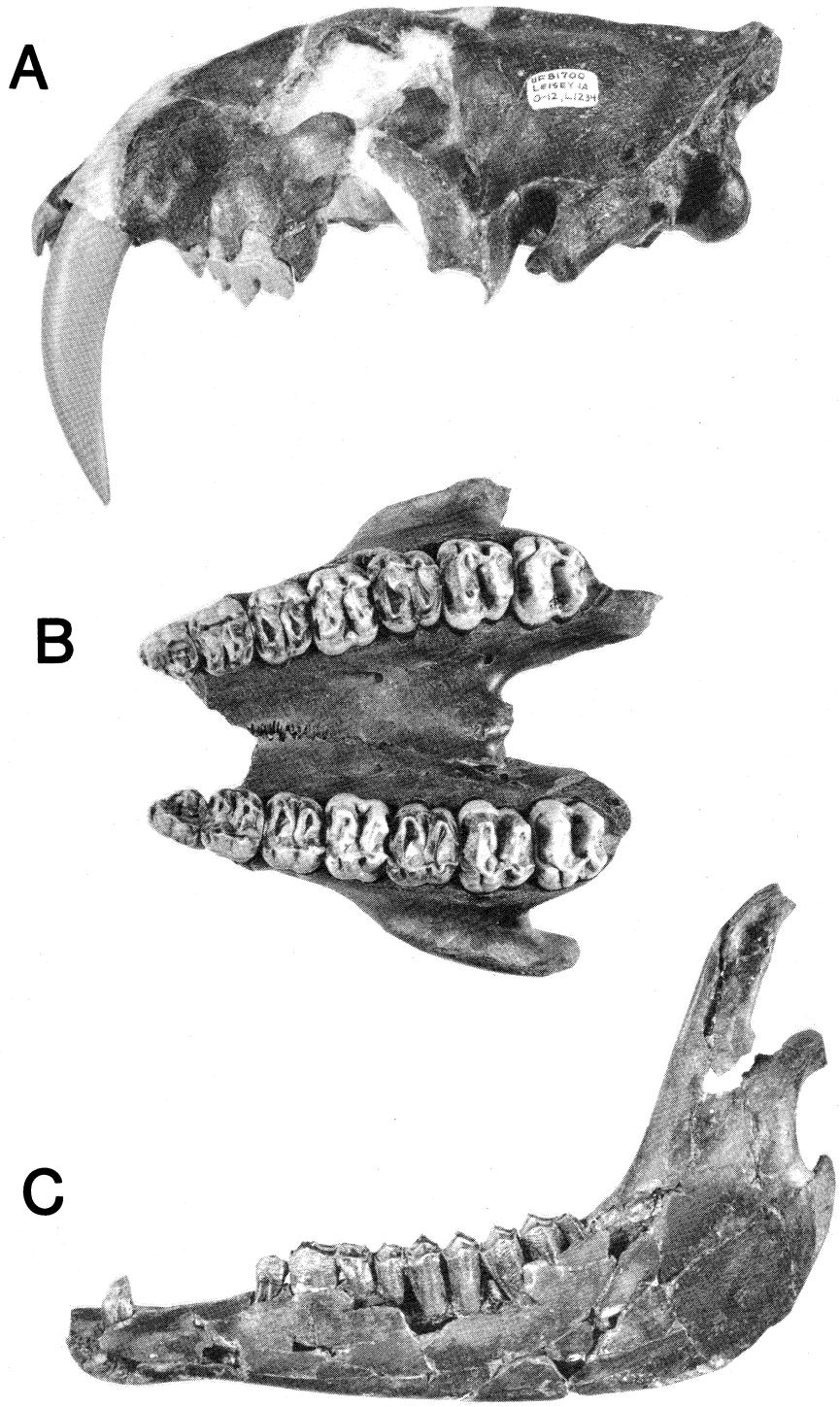

Figure 4. Specimens of three of the important large mammals from the Leisey Shell Pit local fauna. A. Lateral view of a skull of *Smilodon gracilis* from Leisey 1A, UF 81700, approximately 26.5 cm (10.4 inches) in length. The canine is from a different individual, and all of the teeth have been coated for photography. B. Occlusal view of a palate of *Tapirus haysii* from Leisey 1A, UF 84190, approximately 20.0 cm (7.8 inches) in length. C. Lateral view of a left mandible of *Hemiauchenia macrocephala* from Leisey 3A, UF 115503, approximately 28.3 cm (11.1 inches) in length. This is one of the uncommon fully adult individuals recovered from this site.

Three shelled edentates are common elements of the Leisey Shell Pit local fauna, the beautiful armadillo *Dasypus bellus*, a pampathere, *Holmesina* sp., cf. *H. floridanus*, and a new species (and possibly genus) of miniature glyptodont. This tiny glyptodont was apparently common in the late early Irvingtonian of Florida, with other records at Haile 16A, Apollo Beach, the Bone Valley Region, and several shell pit sites along the southwestern Gulf Coast. Individual scutes are about the same size as buckler scutes of *D. bellus*, but are about three to four times as thick, and have the rosette pattern of glyptodonts. Among the hundreds of osteoderms found, no comparably thick movable scutes are known, confirming that this species is not a dasypodid or pampathere (which both possess several rows of movable scutes). Edmund (1987) regarded all pampatheres from Florida as a single lineage that gradually increased in size through time. Edmund (1987, p. 17) referred Blancan specimens to *Holmesina floridanus*, late Irvingtonian and Rancholabrean specimens to *H. septentrionalis*. Early Irvingtonian specimens were referred only to *Holmesina* sp., as they were "...intermediate in size [to the two named species]..." but that "...a new specific name is unwarranted." Unfortunately by this scheme the Leisey sample is left without a species name. The increase in size of this lineage through time noted by Edmund (1987) does not appear to have occurred at a constant rate. The rate of increase was slow during the Blancan and early Irvingtonian, rapid between the early and late Irvingtonian, and then slow again through the Rancholabrean. Thus, if the lineage is to be represented by two species, then the least arbitrary point of separation is between early and late Irvingtonian populations, and the Leisey sample is provisionally referred to *H. floridanus*.

While represented by far fewer numbers of individuals than the large herbivores, the large carnivores add significantly to our knowledge of several early Pleistocene species, especially the gracile saber-toothed cat, *Smilodon gracilis*, and the lesser short-faced bear, *Arctodus pristinus*. The *Smilodon* sample includes one nearly complete skull (Fig. 4A), several other partial crania with complete basicranial regions, several maxillae, about ten mandibles, and many isolated teeth and post-cranial elements. Certainly this is the best sample of this previously poorly known species yet recovered, and morphologically it compares favorably with previously described *S. gracilis* specimens from the late Blancan and early to middle Irvingtonian (Berta, 1987). *Arctodus* is represented by one complete mandible, and several partial rami and isolated teeth. Their smaller size distinguishes them from the giant *A. simus*, and compares favorably with the eastern species *A. pristinus*. The other two most common carnivores at Leisey were *Canis edwardii*, a large coyote-sized dog, and the larger, wolf-sized *Canis armbrusteri*.

The two most common rodents at Leisey are the large aquatic capybara (*Hydrochoerus*) and giant beaver (*Castoroides*). The latter is represented by two partial skulls from Leisey 1A and a complete mandible from Leisey 3B, as well as less complete material. Capybara remains are predominantly post-cranial elements and cheektooth fragments, neither of which are particularly diagnostic. The reference to *Hydrochoerus* rather than *Neochoerus* is made on the basis of size. The biostratigraphically useful microtine group is unfortunately very poorly represented at Leisey. Only two teeth are known, and neither represents the diagnostic lower first molar or upper third molar. One tooth apparently represents a vole (*Microtus*), but can not be identified to subgenus, the other a bog lemming (*Synaptomys*). A mandible referable to the pocket gopher *Geomys* represents the living species *G. pinetis* rather than the very early Irvingtonian *G. propinetis* on the basis of its relatively deep retromolar fossa (Wilkins, 1984). More complete material from Haile 16A, not available to Wilkins in his study, suggests referal of this sample to *G. pinetis* instead of *G. propinetis*. The latter is apparently limited to the very early Irvingtonian. Several mandibles and maxillae of the extinct cotton rat *Sigmodon libitinus* were recovered from Leisey 3A. This species is known elsewhere only from the middle Irvingtonian Haile 16A, and seems to represent an evolutionary stage between *S. curtisi* from Inglis 1A and *S. bakeri* from Coleman 2A (Martin, 1979).

Horses (genus *Equus*) are well represented at Leisey 1A, this being by far the largest single quarry sample of *Equus* from Florida. Species-level systematics of *Equus* are notoriously difficult, especially in Florida which previously lacked adequate samples for detailed study. The Leisey sample demonstrates that there were at least three species of *Equus* present in the Florida Irvingtonian. The most common at Leisey, and the most widespread in Florida (also known from Rigby Shell Pit, Pool Branch, Coleman 2A, and Inglis 1A), is a medium-sized, stout-legged species closely related to *E. conversidens* and *E. scotti*. Hay's (1913) *E. leidyi* may represent this species, but the validity of horse names based on isolated teeth without stratigraphic control (such as *E. leidyi*) is questionable. Also common at Leisey, but rare or absent elsewhere, is a medium-sized, slender-legged species closely related to *E. calobatus* and *E. francisci*. It probably represents an undescribed species of the subgenus *Hemionus*. The third species of *Equus* is rare

TABLE 2. Mammals of the Leisey Shell Pit local fauna, early Pleistocene, Hillsborough County, Florida. The taxa shown as present in the column labelled "Leisey 1" are only those not recorded from a specific site. An "X" indicates a definite identification, "C" a possible identification, "?" a doubtful identification, and "--" an absence.

	LEISEY SITES				
	1	1A	1B	3A	3B
Order Edentata					
Dasypus bellus	--	X	--	X	--
Holmesina sp., cf. *H. floridanus*	--	X	X	X	X
Glyptotherium arizonae	C	--	--	--	--
?Glyptotherium n. sp.	--	X	--	X	X
Glossotherium harlani	--	X	--	X	--
Nothrotheriops sp.	--	X	--	--	--
Eremotherium sp.	X	--	--	--	--
Order Carnivora					
Canis edwardii	--	X	--	--	--
Canis armbrusteri	--	X	X	--	--
Urocyon sp.	--	X	--	--	--
Odobenidae	X	--	--	--	--
Monachus sp.	--	X	--	--	--
Procyon sp.	--	X	--	--	--
Arctodus pristinus	--	X	X	--	X
Mustela frenata	--	--	--	X	--
Lutra sp.	--	X	--	--	--
Panthera onca	--	C	--	--	--
Homotherium sp.	--	X	--	--	--
Smilodon gracilis	--	X	--	--	--
Felis rufus	--	X	--	--	--
Order Rodentia					
Hydrochoerus sp.	--	C	--	--	--
Castoroides ohioensis	--	X	--	--	X
Sigmodon libitinus	--	?	--	X	--
Microtus (sensu lato) sp.	--	X	--	--	--
Synaptomys sp.	--	--	--	X	--
Geomys pinetis	--	X	--	--	--
Order Lagomorpha					
Sylvilagus sp.	--	C	--	X	--
Lepus sp.	--	X	--	--	--
Order Perissodactyla					
Tapirus haysii	--	X	X	X	X
Equus "leidyi"	--	X	X	X	X
Equus (*Hemionus*) n. sp.	--	X	--	--	--
Equus "fraternus"	--	C	--	--	--
Order Artiodactyla					
Mylohyus nasutus	--	C	--	--	--
Platygonus vetus	--	C	--	--	--
Hemiauchenia macrocephala	--	X	--	X	X
Palaeolama sp.	--	X	X	--	--
Odocoileus virginianus	--	X	X	--	X
Order Cetacea					
Stenella sp.	--	C	--	--	--
Odontoceti (genus indet.)	--	--	--	--	X
Mysticeti (genus indet.)	--	X	--	--	X
Order Sirenia					
Trichechus manatus	--	X	--	X	X
Order Proboscidea					
Mammut americanum	--	X	--	--	--
Cuvieronius sp.	--	X	--	X	--
Mammuthus sp.	--	X	X	--	X

at Leisey 1A (two specimens), but well represented at Haile 16A. It is a large-sized taxon, with complex enamel plications, poorly developed or absent infundibula on compressed lower incisors, and deep molar ectoflexids. The old name *E. fraternus* might apply to this species, but it faces the same nomenclatural difficulties as *E. leidyi*. A species heretofore very poorly known that is well represented at Leisey is the giant Pleistocene tapir, *Tapirus haysii* (Fig. 4B). Thus the prediction of Ray and Sanders (1984, p. 296) that Florida would produce diagnostic material of this species is fulfilled. The sample includes complete mandibles, maxillae, basicrania, and post-cranial elements. These demonstrate a close relationship between *T. haysii* and *T. veroensis* of the Rancholabrean.

Five species of artiodactyls representing three families are present at Leisey (Table 2). The absence of the Antilocapridae is significant, as pronghorns are relatively abundant in late Hemphillian, Blancan, and very early Irvingtonian faunas of Florida. With the increased number of late early Irvingtonian sites in the state, the chances that the absence of the family during this interval is an artifact of the fossil record are now small. Inglis 1A is the youngest record of the Antilocapridae in Florida. As noted above, camels are very well represented at Leisey: *Palaeolama* is the most common mammal at Leisey 1A, and *Hemiauchenia* the most common at Leisey 3B (and also quite common at Leisey 1A; Fig. 4C). Every skeletal element of both genera is well represented, although all of the skulls are disassociated into their constituent elements. The *Palaeolama* sample from Leisey is the oldest definite record of the genus in North America (excluding the problematic "*P.*" *guanajuatensis* Dalquest and Mooser, 1980 from the late Hemphillian Ocote local fauna; see Montellano, 1989), and probably predates all South American records as well. Webb (1974) listed the middle Pleistocene Tarija Fauna as the oldest record for the genus. The age of the Tarija Fauna is between 1.0 and 0.7 Ma (MacFadden et al., 1983), and probably slightly younger than Leisey. Both of the common Pleistocene peccary genera of North America are present at Leisey, although *Platygonus* is more common than *Mylohyus*, and represented by more complete material. The two appear to resemble previously described Irvingtonian samples from eastern North America, such as those from Coleman 2A and Cumberland Cave. White-tailed deer, *Odocoileus virginianus*, is the least common of the Leisey artiodactyls, but is nevertheless represented by one nearly complete antler and several toothrows.

Proboscidean remains were also common at Leisey, consisting predominantly of scattered limb elements, vertebrae, ribs, isolated teeth and tusks (generally badly fragmented), and skull fragments. The American mastodon, *Mammut americanum*, was particularly well represented by juvenile teeth; very few adult dentitions were recovered. Mammoth (*Mammuthus*) at Leisey was represented by numerous adult and juvenile teeth. The former are characterized by a lamellar frequency of 4.5 to 6.0 (number of plates per 100 mm), thick enamel (mean thickness of 2.6 mm, s=0.21, n=13), and 15 to 17 plates on the M^3. These features are somewhat intermediate between those of *M. meridionalis* and *M. imperator* as defined by Maglio (1973), and further study is needed for a definite specific allocation. The gomphothere *Cuvieronius* has been identified from Leisey 1A, 3A, and the lower shell bed at Leisey 1, but is the rarest of the three proboscideans in the Leisey local fauna.

The vertebrate fauna from Leisey 1C is distinctly different from the others (Table 3). This assemblage is similar in composition and preservation to vertebrates from the Manatee County Dam, Braden River, and Port Manatee sites in Manatee County and Lockwood Meadows in Sarasota County. The specimens are typically black and heavily waterworn. A late early Hemphillian age (about 6 to 7 Ma) is suggested by the combined presence of *Nannippus minor*, *Neohipparion eurystyle*, and *Cormohipparion ingenuum* (Hulbert, 1988). A spheroidal quartzite pebble was found with these specimens. These are considered diagnostic of the Bone Valley Formation in southern Florida.

AGE OF THE LEISEY SHELL PIT LOCAL FAUNA

The Leisey Shell Pit local fauna is designated as the assemblage of vertebrate taxa recovered from lenses within the Bermont Formation in the three Leisey Shell Pits. It includes species from Leisey 1A, 1B, 3A, and 3B, but not those of Leisey 1C. Also excluded are Rancholabrean vertebrates occasionally recovered from the upper shell bed (Fort Thompson Formation) at Leisey, especially Leisey 2. The age of the Leisey Shell Pit local fauna can be determined through numerous methods, such as biostratigraphic

TABLE 3. Faunal list of vertebrates recovered from the Leisey 1C locality, late Miocene (late early Hemphillian), southwestern Hillsborough County, Florida.

Class Chondrichthyes
Order Selachii
Family Lamnidae
Isurus hastalis
Carcharodon megalodon

Class Mammalia
Order Perissodactyla
Family Equidae
Neohipparion eurystyle
Nannippus minor
Cormohipparion ingenuum
Family Rhinocerotidae
cf. *Aphelops* sp.
Order Cetacea
Family Cetotheriidae, gen. indet.

correlation using macroinvertebrates, microfossils or vertebrates, strontium isotope analysis, and paleomagnetic polarity stratigraphy (Webb et al., 1989). As the fauna consists of both abundant invertebrates and vertebrates, it serves as an important "cross-reference" for chronologies based on marine molluscan assemblages (e.g. Blackwelder, 1981) and on terrestrial mammals (North American Land Mammal Ages; see e.g. Savage, 1951). The microfossils (e.g., foraminifera, ostracods, or nanoplankton) from Leisey have not yet been studied.

Using mammalian taxa as biostratigraphic indicators clearly places the Leisey Shell Pit local fauna within the Irvingtonian Land Mammal Age (0.3 to 1.9 Ma; Lundelius et al., 1988). Furthermore, the absences of taxa typical of Blancan and/or very early Irvingtonian faunas in Florida (e.g., *Trachemys platymarginata*, *Nannippus peninsulatus*, *Capromeryx arizonensis*, *Chasmaporthetes ossifragus*), the stages of evolution of *Geomys* (Wilkins, 1984) and *Sigmodon* (Martin, 1979), and the presence of *Mammuthus* indicate that the Leisey Shell Pit local fauna is younger than Blancan or earliest Irvingtonian. Additional general indicators of an Irvingtonian age are the presence or stage of evolution of ?*Glyptotherium* n. sp., *Holmesina*, *Arctodus pristinus*, *Lutra*, *Canis edwardii*, *Canis armbrusteri*, *Castoroides ohioensis*, *Tapirus haysii*, *Platygonus* cf. *P. vetus*, and *Palaeolama*. The presence of *Smilodon gracilis* rather than the larger, more advanced late Irvingtonian and Rancholabrean *S. populator* (sensu Berta, 1985; = *S. fatalis* and *S. floridanus*) indicates a pre-late Irvingtonian age, as does the primitive grade of the *Mammuthus* and *Sigmodon*. The Leisey mammalian fauna seems to best indicate a late early Irvingtonian age, or about 1.5 to 1.0 Ma. The two stratigraphically lowest sites, Leisey 1B and Leisey 3B are indistinguishable in age from the main site on the basis of their faunal composition (Table 2). Both contain *Mammuthus*, *Tapirus haysii*, *Arctodus*, and an intermediate-sized *Holmesina*, all indicative of Florida Irvingtonian faunas. Therefore, base of the lower shell bed at Leisey is less than 1.7 Ma.

TAPHONOMY AND PALEOECOLOGY

As with the systematic section, this discussion of the taphonomy and paleoecology of the Leisey Shell Pit is preliminary and predominantly refers to the best studied site, Leisey 1A. Although many analyses remain to be done, our observations suggest a paleoecological model that will be repeatedly tested and refined with future work. Morgan et al. (in prep.) provide a much more detailed study of the paleoecology of the invertebrate fauna. Most previous taphonomic studies of vertebrates (e.g. Clark et al., 1967; Behrensmeyer, 1975; Hanson, 1980) have focused on continental depositional environments (fluvial, lacustrine, etc.), although Bishop (1980) and Hendey (1981) discussed fossil accumulations in environments at continental margins. At Leisey, continental and marine influences combined to produce a taphonomically complex fossil (invertebrate and vertebrate) assemblage.

There are several indicators that the bones were deposited in a low energy environment. Bone-producing lenses were the only parts in the section to contain any sizable fraction of mud. Iron staining was common on both shells and bones, and in a few cases there were encrustations of pyrite crystals. Preliminary analysis of orientation data (bearing and plunge) indicated that the bones were lying without any preferred direction, generally at low angles (Fig. 5A & 5B). All of the major elements for the medium to large-sized mammals were found (i.e. all three transport groups of Voorhies, 1969), indicating that currents must have been relatively low at the site of deposition (Behrensmeyer, 1975). However, the rarity of small terrestrial taxa could indicate slight water movements (Dodson, 1973), perhaps those associated with tides. Although some of the shells were certainly transported by storms, tides and currents, as evidenced by breakage and abrasion, the well-preserved condition of most of the shells, and the high frequency of bivalves preserved as articulated valves also suggest quiet water conditions.

The vertebrate fauna at Leisey can be divided into two major subfaunas, each with its own ecological and taphonomic histories. One is interpreted to be the animals that lived at or very near the site of deposition. This subfauna is composed of most of the sharks and fish (including the very abundant *Atractosteus spatula*), the diverse aquatic avifauna, and perhaps some of the turtles. This suite of taxa is represented at Leisey by many small fish vertebrae and spines, and delicate bird bones were routinely recovered undamaged or nearly so. This subfauna is interpreted to be a biocoenose, to have undergone little or no taphonomic sorting, and (in conjunction with the invertebrate fauna, see below) as giving the best clues as to the paleoenvironment at the site. The second major subfauna is composed mainly of terrestrial mammals and reptiles, but also by the freshwater taxa (e.g. *Hydrochoerus*, most of the turtles, especially *Trachemys* and *Apalone*) and the rare terrestrial birds. This assemblage is clearly a taphocoenose (sensu Shipman, 1981) and is comparable to the "distal community" of Shotwell (1955). This subfauna shows a much greater bias against smaller sized taxa, and a much higher degree of water-wear and transport damage than does the previously described subfauna. Bone surfaces of members of this group display many features indicating subareal exposure prior to transport and burial. These include bite marks of mammalian carnivores or scavengers, weathering cracks, and numerous scratches caused by trampling. The different sites at Leisey vary in the proportion each of these subfaunas contributed to the whole fauna, and in the degree of bias against smaller nonmarine vertebrates. Leisey 3A has a much richer small vertebrate fauna than Leisey 1A.

The diverse and abundant terrestrial fauna of Leisey 1A is represented predominantly by thousands of fragments, water-worn articular ends and isolated teeth. However, while numerically a small percentage of the total number of bones, there are also thousands of complete or only slightly damaged specimens (excluding the effects of post-burial compaction). The more complete material includes numerous partial associated skeletons. For example, elements belonging to a single carapace of a tortoise or the major elements of the forelimb of a sloth were found within a few meters of one another. Also parts of single elements (most recognizable were right and left dentaries from the same individual) were often found separated, some displaced only a few millimeters, others up to several meters (Fig. 5C). No articulated skeletons were recovered. These well preserved, associated specimens would at first seem to have been transported less than the numerous water-worn fragments with which they were interspersed. However, the interpreted paleoecology of the site, a coastal mangrove bay (see below), makes it unlikely to have been home to vast herds of horses, llamas and peccaries. While some of the large mammals might in fact have died at or near the site, an alternative and more likely source for the well preserved, associated individuals would be from carcasses floating downstream. After deposition at the site, they would then rot and disarticulate. Low water currents at the site allowed only minimal disassociation. The only elements of the large ungulates notably underrepresented at the site were the smallest of the carpal and tarsal bones, and the relatively less dense distal phalanges (hooves), that may have floated away. A similar model was proposed by Hendey (1981) to concentrate associated remains of terrestrial vertebrates into near-marine marsh, tidal flat, and channel environments at Langebaanweg (early Pliocene of South Africa). Klein (1982) studied the population structure of several of the taxa from Langebaanweg and found both attritional and catastrophic assemblages. At Leisey 1A, both the llama and the equid populations contain high percentages of both juveniles and aged individuals with heavily worn dentitions. Pending detailed study, they are considered to be attritional assemblages caused by long term, natural mortality. Juvenile individuals of other mammalian species were also very common. The situation is substantially different at Leisey 3A. There almost all of the relatively complete macrovertebrate elements

belonged to a single species, *Hemiauchenia macrocephala*. Other mammals were represented only by specimens broken and worn by weathering and fluvial transport. The *Hemiauchenia* specimens show no signs of weathering, are undamaged except for postburial compaction, and appear to represent disarticulated and partially disassociated individuals. The majority of individuals were one to two year old juveniles and subadults; only a few true adults were recovered. This age distribution suggests a catastrophic assemblage. The cause of death is purely speculative, but based on their entombment in estuarine sediments, one possibility is that a herd of llamas were caught in a flood and washed downstream.

Important to an understanding of the depositional environment at Leisey is an analysis of the molluscan fossils that are found with the bones. In order to obtain adequate samples of both microvertebrates and invertebrates, we collected over a metric ton of matrix from two of the areas of richest bone concentration at Leisey 1A. Morgan et al. (in prep.) identified 156 species of invertebrates from this horizon: 147 species of mollusks (80 gastropods, 65 bivalves, and two scaphopods); a boring sponge; two colonial scleractinian corals; one bryozoan; one polychaete worm; one echinoid; two crabs; and at least one species of barnacle. Although there are more species of gastropods, most are small and uncommon; bivalves overwhelmingly dominate the molluscan fauna both in numbers and average size of individuals. The medium-sized bivalves *Chione cancellata* and *Carditamera floridana* are the two most abundant marine mollusks in the bone bed, the former species comprising approximately half of the volume of shells in this unit. The most abundant species of gastropod, *Planorbella scalaris*, is actually a freshwater inhabitant, as are two other snails common in the bone bed, *Physella* sp. and *Hyalopyrgus aequicostatus*. As these three are intolerant of even brackish water, it is hypothesized that they were transported along with the terrestrial and freshwater vertebrates into a marine depositional environment. The majority of the marine shells are very well preserved. This, in conjunction with the high frequency of articulated valves of the clams, indicates that they had minimal or no post-mortem transport, and that they should be good indicators of the depositional environment of the bone bed.

Most species of mollusks from Leisey 1A are identical to living species, and thus the preferred habitats of the modern forms are used to reconstruct the overall paleoenvironment at the site. The majority of the mollusks present live today in water approximately 1-2 m in depth, and many prefer protected bays and lagoons. Over 20% of the gastropods in the bone bed, including more than half of the most common marine species, occur in association with marine grass beds, while the remainder favor a sandy mud substrate or mudflats. Sand-dwelling species are present, but are considerably less common. This agrees with the proportions of clastic sediments in the bone bed, in which silt and mud have larger fractions than sand-sized grains. In addition, seven of the most common mollusk species live attached to a hard substrate. With the absence of rocks or a hard bottom in the Leisey environment, these species were most likely attached to other shells, mangrove roots, and bones. In fact, oysters (*Ostrea*) and bryozoans were found attached to some of the fossil bones. The overall depositional environment suggested by the marine molluscan fauna (and also either supported or at least not falsified by members of the first vertebrate subfauna described above) is a shallow (about 1-2 m), protected bay with near normal marine salinity, having extensive marine grass beds, and with a substrate composed primarily of mud and shells. A large, slow-moving river would probably have emptied into the bay, accounting for the periodic influx, possibly during floods, of freshwater and terrestrial organisms.

Also critical to our concept of the paleoenvironment at Leisey 1A is the interpretation of the origin of many vertical, near-vertical, and to a lesser extent horizontal cylindrical objects commonly encountered during the excavation of the "hard layer" and the bone bed. These varied in diameter from about 2 to 50 cm, and often extended from the base of the bone bed to the top of the "hard layer." In cross-section, they have a more solid outer layer surrounding a very porous center with many longitudinal channels. Typically they were arranged in the field such that a very large vertical structure was surrounded by many smaller vertical and angled ones. This suggested that they were the remains of *in situ* mangrove root systems. Their internal structure greatly resembles that of previously identified fossilized black mangrove (*Avicennia nitida*) roots from Key Biscayne, Florida (Hoffmeister, 1974, figure 34). Black mangroves grow today along Tampa Bay and extend several kilometers up the mouths of local rivers. Little Manatee River, less than a kilometer from the site, is a typical example. Mangroves are indicators of at least subtropical temperatures and brackish to coastal marine, very shallow water environments. Vertebrate fossils were occasionally found in contact with the mangrove roots at high angles, suggesting that the bone had been

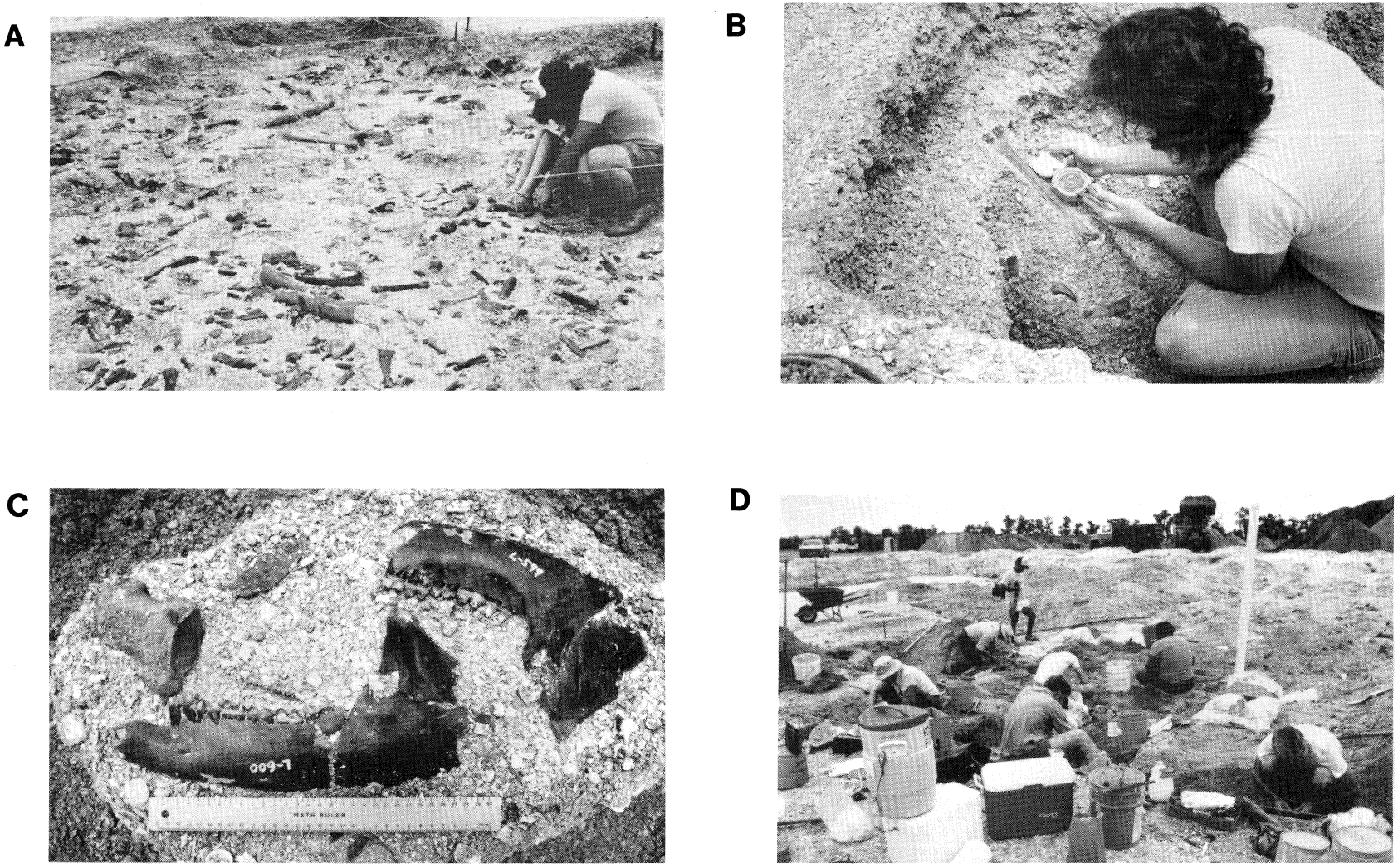

Figure 5. Field photos of Leisey 1A taken during 1984. A. View of the site in April showing random distribution of bones. B. Gary Morgan taking the bearing of a camel metapodial with a Brunton compass. C. The right and left dentaries of *Tapirus haysii* from the same individual that became separated prior to burial. D. View of the site in September showing typical field conditions. The crew consists of members of the Tampa Bay Mineral and Science Club and Florida Museum of Natural History personnel.

caught in the root system, and that the mangroves and the fossils were contemporaneous. The only other plant remains found at Leisey 1A were numerous seeds of the sabal or cabbage palm (*Sabal palmetto*), which still grows in profusion alongside black mangroves in southern Florida. Mangrove roots and palm seeds were absent at the other Leisey sites, suggesting slightly different depositional environments. Macrobotanical remains, including wood and pine cones, were common in the lower parts of the lower shell bed, especially Leisey 3B.

Our model for the depositional setting of the Leisey Shell Pit 1A vertebrate site is a shallow coastal mangrove-lined bay located adjacent to, or at the mouth of a river (possibly the ancestral Little Manatee River). Vertebrate remains carried by the river were deposited into the bay, where local conditions favored concentration and preservation of the bones. Minor currents, scavengers, and/or tidal activity were sufficient to remove most of the small vertebrate remains and to disassociate larger vertebrate carcasses. After a relatively short period of geologic time, the vast influx of terrestrial vertebrates ceased, and the hard layer was deposited, probably during a regression. The coastal plain of Florida must have consisted of a productive woodland-savanna mosaic to support such a diverse and apparently numerous large herbivore fauna. A subtropical climate, more equable but not very different in terms of temperature from the present, is indicated by the presence of mangroves, sabal palm, large *Geochelone*, *Alligator*, *Tapirus*, and the shelled edentates *Dasypus*, *Holmesina*, and glyptodont.

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