NEW PLEISTOCENE (RANCHOLABREAN) VERTEBRATE FAUNAS FROM COASTAL GEORGIA

RICHARD C. HULBERT, JR.1 and ANN E. PRATT²

¹Department of Geology and Geography, Georgia Southern University, Statesboro, Georgia 30460-8149; ²Department of Biology, Georgia Southern University, Statesboro, Georgia 30460-8042

ABSTRACT—Four new late Pleistocene faunas have been collected in Chatham County, Georgia, in the vicinity of Savannah. Together they have produced 103 vertebrate taxa (12 chondrichthyans, 25 actinopterygians, 7 amphibians, 20 reptiles, 4 birds, and 35 mammals), of which at least 14 are extinct. About 75 percent of these taxa are reported for the first time as fossils from coastal Georgia. The Isle of Hope, Mayfair, and Jones Girls sites are numerically dominated by neritic marine fossils, both vertebrate and invertebrate, implying that their original depositional environment was estuarine or nearshore marine. The less common, terrestrial component of these faunas was either brought in by fluvial and tidal current transport or introduced by reworking of underlying continental sediments. These sites apparently date to the last interglacial (oxygen isotope Stage 5), at a time when relative sea level was close to or slightly above current values. This age assignment is supported by the composition of the fauna and uranium-series and radiocarbon dating. The fourth new site, Porters Pit, is a fluvial channel lag deposit of coarse clastic sediments and a chronologically mixed assemblage of Miocene, Pliocene, and Pleistocene fossils. It dates to a period of fluvial down-cutting during an eustatic sea-level lowstand.

The Isle of Hope Site contains the first rich vertebrate microfauna from coastal Georgia. The most significant aspects of this fauna are the presence of several extralimital taxa (e.g., *Ambystoma maculatum*, *Blarina brevicauda*, *Microtus pennsylvanicus*, *Neofiber alleni*), and the dominance among the small rodents by arvicolines rather than peromyscines and sigmodontines. An unlikely member of the fauna is the small felid *Leopardus*. Although represented by only a single element, a mandible, it differs morphologically from modern members of the genus and the late Pleistocene species *Leopardus amnicola*.

INTRODUCTION

The first discovery of fossil vertebrates from coastal Georgia. on the southwestern end of Skidaway Island, Chatham County (Fig. 1), dates to 1823 (Mitchell, 1824; Hay, 1923). In the 1830s, a nearly complete skeleton of Mammut americanum was excavated from a salt marsh near Heyner's Bridge, about 5.5 km west-northwest of the original Skidaway Island site (Lipps et al., 1988). Beginning in 1838, similar fossils were found in the vicinity of Brunswick in Glynn County during construction of a canal (Fig. 1). As a result of reports by Lyell (1845, 1849) and other authors (e.g., Hodgson, 1846; Leidy, 1855), the regions around both Savannah and Brunswick temporarily became well known for their Pleistocene vertebrate fossils. The taxonomic diversity of these early discoveries was actually quite low, with the reported faunas consisting for the most part of a few large ungulates and edentates (Table 1). However, Eremotherium mirabile and Mammuthus columbi, two classic members of the extinct North American Pleistocene megafauna, were named on the basis of specimens collected from coastal Georgia during this time frame.

For well over a century relatively little in the way of published studies or large-scale paleontological excavations occurred in the region. Specimens collected by various individuals over the years were either lost or never studied by professional paleontologists. Hurst (1957) and Lipps et al. (1988) both discussed the historical aspects of vertebrate paleontology in coastal Georgia. The lone "modern" site from the region listed in Kurtén and Anderson's (1980) extensive review was Watkins Quarry in Glynn County. This locality yielded only seven species of mammals (Table 1) and was never formally described. To date, the only published records of Watkins Quarry are an abstract and an account in a field guide (Voorhies, 1971, 1973) and a brief mention in Ray (1979: 5–6). No sites from coastal Georgia were listed by Holman (1995).

An additional locality from coastal Georgia, not mentioned by Kurtén and Anderson (1980), is the Turtle River Site near Brunswick (Fig. 1; Frey et al., 1975). This site contained a limited assemblage of Pleistocene fossil vertebrates (listed in Table 1), mostly recovered from spoil piles of dredged sediments. Prior to our work, the Turtle River dredgings had produced the most diverse Pleistocene fauna (14 mammalian species, of which eight are extinct) from the Georgia Coastal Plain.

We report here four new fossil vertebrate localities from the Savannah metropolitan area (Fig. 1). Three of these, the Mayfair, Isle of Hope, and Jones Girls sites, are close to the original nineteenth century fossil locality on Skidaway Island, which we refer to as the Fossilossa Site, following Hodgson (1846). The remaining new locality, Porters Pit, is located about 15 km northwest of the others, and also represents a distinctly different environment of deposition. Of the new localities, the Isle of Hope Site has produced the richest vertebrate fauna (Tables 1, 3, and 4), by far the most diverse yet from the Georgia Coastal Plain, while the Jones Girls Site was the most informative of the four with regard to accessible stratigraphy and geochronology. Excavations at the latter concluded in 1996 and processing of its specimens is not completed; all discussions regarding this site are thus preliminary.

When combined, the four new localities have produced a total of 103 Pleistocene vertebrate taxa, increasing the number known from coastal Georgia by 74. At least 14 of the total are extinct (12 mammals and two reptiles). In the following sections, we document the geology, geochronology, and paleoecology of these four fossil sites, and the diversity and morphology of their constituent vertebrate faunas.

MATERIALS AND METHODS

All vertebrate fossils discussed from the Isle of Hope, Mayfair, Jones Girls, and Porters Pit sites are housed in the Georgia Southern Museum fossil collection, Statesboro. Catalogue numbers for these specimens are preceded by the acronym **GSM**. To identify the fossils, we used comparative modern specimens in our own collection, as well as those from the Herpetology,

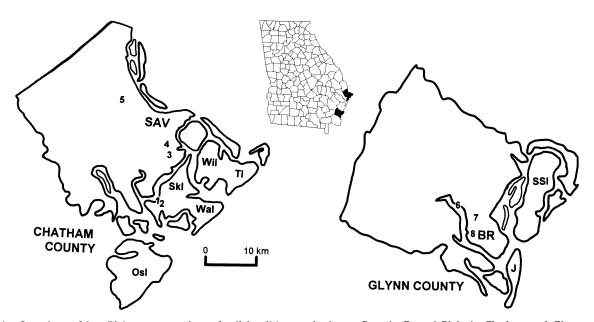


FIGURE 1. Locations of late Pleistocene vertebrate fossil localities on the lower Georgia Coastal Plain in Chatham and Glynn counties. 1, Fossilossa Site; 2, Jones Girls Site; 3, Isle of Hope Site; 4, Mayfair Site; 5, Porters Pit Site; 6, Turtle River Dredgings; 7, Watkins Quarry; 8, Brunswick Region. Geographic abbreviations: **BR**, Brunswick; **J**, Jekyll Island; **OsI**, Ossabaw Island; **SAV**, Savannah; **SkI**, Skidaway Island; **SSI**, St. Simons Island; **TI**, Tybee Island; **WaI**, Wassaw Island; **WiI**, Wilmington Island.

Mammalogy, Vertebrate Paleontology, and Zooarchaeology collections of the Florida Museum of Natural History, Gainesville (UF). Some were also compared with vertebrate fossils in the UF collection. Modern geographic ranges and habitats used in paleoecologic discussions were obtained from Golley (1962), Dahlberg (1975), Hall (1981), Webster et al. (1985), and Ashton and Ashton (1988). All measurements are in millimeters. USNM refers to specimens in the collection of the National Museum of Natural History, Washington, DC; ROM to the Royal Ontario Museum, Toronto.

Detailed locality information is filed in the Paleontology Collection of the GSM. The approximate locations of the four sites are: Isle of Hope, 31°59'N, 81°4'W; Mayfair, 32°0'N, 81°6'W; Jones Girls, 31°55'N, 81°4'W; and Porters Pit, 32°5'N, 81°10'W.

Specimens from the Porters Pit and Mayfair sites were collected by Mr. John Heard of Savannah in the 1980s and donated to the GSM. Neither site is presently accessible for stratigraphic or paleontologic study. The Isle of Hope Site is located on both banks of a sharp meander of a tidal channel flowing through the salt marsh that separates the Isle of Hope from the mainland. Early collections from this site (in the 1980s) were made during the construction of a boat pier on the outer bank of the meander, or directly from the channel bed during exceptionally low tides. Many specimens found during this phase were donated to the GSM by the landowners and John Heard. The outer bank was subsequently covered with riprap to protect it from erosion and is no longer accessible for collecting. Since the late 1980s, GSM paleontologists and John Heard have collected specimens from the modern point bar and inner bank of the channel. In this area, the vertebrate fossils are found intermingled with Pleistocene, Holocene, and modern invertebrates (predominantly mollusks and barnacles), in what is clearly a reworked, temporally mixed deposit. The possibility exists that the age of some of the vertebrates from this region of the site is actually Holocene, but these are not regarded to be a significant portion of the fauna, because of uniformity in preservation among the specimens and lack of Old World contaminants (such as Sus, Mus, Rattus, or Bos) introduced subsequent to the European discovery of North America.

The Jones Girls Site is located in two shallow ponds excavated in 1995 and 1996 on the southwestern end of Skidaway Island (Fig. 1). Vertebrate fossils are uncommon at this site, although it has produced a diverse, well-preserved, estuarineshallow marine molluscan fauna. The vertebrate fauna is predominantly marine, and includes chondrichthyans, actinopterygians, and cetaceans. Only two specimens of terrestrial vertebrates, a rodent calcaneum and a snake vertebra, have been recovered. Pumping during excavations exposed a 3 to 4 m thick section, allowing detailed stratigraphic analysis, a unique opportunity among the Savannah area vertebrate fossil sites that we have studied. The Jones Girls Site is also the only site in the region that has produced the necessary specimens for geochronologic analysis beyond the limits of carbon-14 dating: pristine, articulated valves of the clam Mercenaria mercenaria for amino acid racemization analysis and unaltered specimens of the stony coral Astrangia danae for uranium-series dating.

Large samples (100s of kg) of fossiliferous matrix from both the Jones Girls and Isle of Hope sites were screen-washed to recover small vertebrates and mollusks. The sediment from the latter was washed through nested screens with openings of 39 mm^2 and 2 mm^2 . The concentrate was then dried and sampled for vertebrates and complete invertebrates. A limited amount was also passed through a screen with openings of 1.1 mm^2 . Matrix from the Jones Girls Site was washed through all three screen sizes.

GEOLOGIC SETTING

The Quaternary sediments of coastal Georgia were reviewed by Hoyt and Hails (1974), Howard and Frey (1980), Huddlestun (1988), and Markewich et al. (1992). They provided discussions of the older literature. Although differing in stratigraphic methodology, they agreed that late Quaternary sedimentation in coastal Georgia mostly occurred in environments similar to those observed today. These include short barrier islands with sandy beaches separated by sounds and tidal channels, backbarrier salt marshes, shallow neritic marine facies, and fluvial channels. A possible difference is the greater extent of back-

TABLE 1. Occurrences of Pleistocene land mammals in coastal Georgia. The first five sites are in Chatham County, the remaining three in Glynn
County (Fig. 1). References for faunas are: Fossilossa Site, Hay (1923); Savannah River, Lipps et al. (1988); Brunswick Area, Hay (1923) and
Lipps et al. (1988); Watkins Quarry, Voorhies (1971, 1973) and Ray (1979); and Turtle River Dredgings, Frey et al. (1975). Data from remaining
sites are original and reported here for the first time. An X indicates the definite presence of the indicated taxon, a ? indicates the possible presence
of that taxon or a closely related form.

	Isle of Hope Site	Mayfair Site	Fossilossa Site	Porters Pit	Savannah River	Brunswick area	Watkins quarry	Turtle River dredg.
Didelphis virginiana	X						Х	
Dasypus bellus	Х	Х					Х	
Holmesina septentrionalis		Х						Х
Eremotherium laurillardi	Х		Х	Х	Х	Х	Х	Х
Paramylodon harlani	Х		Х			Х		
Megalonyx sp.					Х			
Blarina brevicauda	Х							
Blarina carolinensis	Х							
Scalopus aquaticus	Х							
Ursidae	Х							
Procyon lotor	Х	Х						
Lutra canadensis	Х							
Leopardus sp.	Х							
Lynx rufus	Х							
Glaucomys volans	Х							
Sciurus carolinensis	Х							
Spermophilus sp.								Х
Castor canadensis	Х	Х						
Castoroides ohioensis					Х	Х		
Oryzomys palustris	Х							
Sigmodon hispidus	Х							
Neotoma floridana	Х							
Peromyscus polionotus	?							
Geomys pinetis								Х
Neofiber alleni	Х							Х
Synaptomys australis	Х							
Microtus pennsylvanicus	Х							
Microtus pinetorum	Х							
Neochoerus pinckneyi		?		?	Х			
Hydrochaeris holmesi					Х	Х		Х
Sylvilagus floridanus	Х	?						?
Sylvilagus palustris	Х							
Mylohyus fossilis	Х							
Palaeolama mirifica		Х						?
Bison sp.	Х		Х			Х		X
Odocoileus virginianus	x	х		Х	Х	x	Х	X
Tapirus veroensis	X	x			x	x	X	
Equus sp.	X	X	Х	Х	x	x	x	Х
Mammut americanum	X	X	X	x	X	x		X
Mammuthus columbi		x	x	x	x	x	х	x
Total taxa	31	12	6	6	10	10	7	13

barrier lagoons at times during the Pleistocene (Huddlestun, 1988). Ideally, each of these depositional environments can be distinguished on the basis of grain size and composition, sedimentary structures, bed geometry, and fossil content (Hoyt and Hails, 1974). However, bioturbation and physical reworking of sediments and fossils are common processes in this region. These, together with rapid lateral facies changes, limited number of outcrops, and extensive erosion during sea-level low-stands, combine to make local stratigraphy and correlations more difficult than they would first appear.

The vertebrate localities under study fall into two geographically and geologically discrete groups, which will be discussed separately. The Mayfair, Isle of Hope, Jones Girls, and Fossilossa sites are located seaward (east) of the Pamlico barrier island complex (as mapped by the Georgia Geological Survey, 1976), and the vertebrate fossils in each were found near or slightly below modern mean sea level. Also, in each case, the vertebrates were associated closely with an invertebrate fauna dominated by estuarine and neritic species of bivalves and gastropods (Table 2). The mollusk shells lying directly under the vertebrate-producing bed at the Fossilossa Site were listed in Hodgson (1846), and described by Lyell (1849) as belonging to extant, marine species, a description that also applies to the mollusks found at the other sites (Table 2).

The original stratigraphic relationships between the marine shells and the terrestrial vertebrates at the Mayfair and Isle of Hope sites can no longer be determined by study of in situ sediments. Several possibilities exist. First, the terrestrial and freshwater vertebrates could have been transported by fluvial and tidal processes into the marine realm, and deposited contemporaneously in the same stratigraphic unit as the marine shells and vertebrates. Second, because modern shell concentrations on the Georgia coast frequently contain reworked Pleistocene (and occasionally Tertiary) fossils (Frey et al., 1975; Henderson and Frey, 1986), the terrestrial fraction of these faunas could have been reworked into the marine deposits from preexisting beds. Finally, the terrestrial fossils might have originally been deposited on top of a shell bed during a regression, as observed at the Fossilossa Site; later the strata could have been mixed together by reworking or human activities. These hypotheses are not mutually exclusive. More field investigations, in particular the discovery of undisturbed sediments, are needed to test these hypotheses. The complete absence of TerTABLE 2. Marine mollusks present at three late Pleistocene vertebrate localities in eastern Chatham County, Georgia. All taxa present at either the Isle of Hope Site or Mayfair Site (or both) are listed; the much more diverse molluscan fauna of the Jones Girls Site is not listed in its entirety. Voucher specimens are housed in the invertebrate paleontology collections of the Georgia Southern Museum and the Florida Museum of Natural History.

	Isle of Hope Site	Mayfair Site	Jones Girls Site
Gastropoda		·····	
Busycon carica (Gmelin)	х		Х
Crepidula fornicata (Linné)		Х	Х
Epitonium rupicola (Kurtz)	Х		Х
Eupleura caudata (Say)	Х		Х
Melongena corona (Gmelin)		Х	
Oliva sayana Ravenel	Х	Х	Х
Polinices duplicatus (Say)	Х	Х	Х
Terebra dislocata (Say)	Х	Х	Х
Bivalvia			
Abra aequalis (Say)	х		Х
Anadara brasiliana (Lamark)	Х		Х
Anadara ovalis (Bruguiere)	Х		Х
Anadara transversa (Say)	Х		Х
Anomia simplex Orbigny	Х		Х
Divaricella quadrisulcata Orbigny	Х		Х
Donax variabilis (Say)	Х	Х	Х
Mulinia lateralis (Say)	Х	Х	Х
Noetia ponderosa (Say)	Х		Х
Nucula proxima Say	Х		Х
Pleuromeris tridentata (Say)	Х		Х

tiary shark species at these two sites indicates that the presence of any reworked, pre-Pleistocene fossils is unlikely.

The main shell-bearing layer at the Jones Girls Site consists mostly of a mixture of fine to medium-sized, rounded to subangular quartz sand grains, and the shells or shell fragments of mollusks and other invertebrates (such as barnacles, bryozoans, echinoids, coral, and serpulid worm tubes). Also present are lesser amounts of muscovite, feldspar, phosphate, clay, and peat. The shell bed is more than a meter thick in places. It underlies beds of unfossiliferous, micaceous quartz sand, and overlies either dark brown peat or greenish gray clay. In the shell bed, bivalves are much more numerous than gastropods, and consist almost exclusively of single valves. There is enormous variation in shell preservation, from rounded, small (sandsized) fragments to pristine, glossy, complete shells, suggesting a complex taphonomic history. Species composition and relative representation are similar to modern shell accumulations off the Georgia coast in tidal inlet channels (Henderson and Frey, 1986), in particular the numerical dominance of the small clam Mulinia lateralis (Say). In general, the section at the Jones Girls Site resembles descriptions of backbarrier and foreshore facies in the Wando Formation, coastal South Carolina (Mc-Cartan et al., 1980).

The Porters Pit Site is located landward of those just discussed (Fig. 1), to the west of the Pamlico barrier island complex. Its clastic sediments are much coarser than those of the other sites, ranging in size from coarse sand to medium gravel. They consist predominantly of quartz, chert, or quartzite fragments, with common accessory grains of feldspar, apatite, and garnet. These sediments are interpreted to be fluvial in origin, and probably were deposited during a glacial sea-level lowstand when there was extensive erosion of Piedmont and Coastal Plain rocks as a result of a lowered base level. The fossils recovered from Porters Pit and nearby gravel quarries in western Savannah and Garden City are well mixed chronologically, with Miocene, Pliocene, and Pleistocene species all represented. The pre-Pleistocene fossils evidently eroded out of beds of the Raysor, Coosawatchie, Marks Head, and Parachucla formations, which are all found up stream from the Savannah region (Huddlestun, 1988). The marine component of these older fossils includes the sharks Carcharodon megalodon, Isurus hastalis, and Hemipristis serra, the crocodile Gavialosuchus americanus, the dugong Metaxytherium, the sperm whale Scaldicetus, and the bivalves Chesapecten septenarius (Say) and Ostrea sculpturata Conrad. A few terrestrial, pre-Pleistocene vertebrates have also been recovered from this region, mostly hipparionine horses and rhinocerotids. Most of the pre-Pleistocene specimens are water-worn to varying degrees and highly phosphatized. Pleistocene vertebrates are actually less common than the older specimens in these deposits, and consist of isolated teeth or tooth fragments and robust skeletal elements. The relative age of these Pleistocene fossils compared with those of the sites in eastern Chatham County is unclear, but apparently they differ, because the former most likely date from a period of low sea level and the latter from a highstand. Cores on the Isle of Hope show that a zone of coarse sand and gravel, similar to the sediments at Porters Pit, underlies the finer grained, interfingering sand and clay deposits (Furlow, 1969). This zone lies at an elevation of about 13 to 20 m (40 to 60 feet) below modern sea level and locally forms the base of the Pleistocene. However, there is no evidence to correlate the gravel deposits from the two regions.

NONMAMMALIAN PLEISTOCENE VERTEBRATES FROM THE SAVANNAH REGION

The published record of Pleistocene fish, amphibians, reptiles, and birds from the Savannah region is extremely scanty. This is somewhat surprising considering their abundance in extant faunas of the region, and must reflect a bias in favor of mammals in past investigations. Prior records include those of unspecified sharks by Hurst (1957), Henry and Hoyt (1965), and Markewich et al. (1992), and the description of a new species of box turtle, *Terrapene canaliculata*, by Hay (1907). This species is not now regarded as valid (Auffenberg, 1958; Milstead, 1969; Holman, 1995).

The fossil chondrichthyans and actinopterygians from the Isle of Hope and Mayfair sites are listed in Table 3. The large number identified only to the generic, familial, or even higher taxonomic level is a function of the fragmentary, nondiagnostic nature of the majority of the specimens (mostly isolated vertebrae and teeth) and limitations of comparative material available to the authors. Otoliths are also present at the Isle of Hope and Jones Girls sites, but have not been identified. Fish from Porters Pit are not listed, as in most cases it is not possible to distinguish between Pleistocene and pre-Pleistocene occurrences, except for those whose chronologic ranges do not include the Pleistocene, such as Carcharodon megalodon. Excluding such obvious pre-Pleistocene species, the only taxon from Porters Pit not listed in Table 3 is the sturgeon Acipenser sp. This record is based on four osteoderms, GSM 93. Only a part of the matrix from the Jones Girls Site has been fully processed, and the fish specimens have not yet been studied. Most are teeth or vertebrae of small species. Only the presence of Rhizoprionodon, Carcharius taurus, rays (Dasyatidae and Myliobatidae), Lepisosteus, and a diodontid can now be confirmed from this locality.

Several aspects of the Pleistocene ichthyofauna from these coastal sites are worthy of discussion. First is the much greater relative abundance of these specimens compared to those of terrestrial fossils, particularly at the Isle of Hope Site. Of the identified species (Table 3), all are taxa that inhabit nearshore coastal waters, sounds, estuaries, or salt marshes. The gar *Lepisosteus* is the only fish listed in Table 3 generally regarded as a freshwater inhabitant, but Dahlberg (1975) noted the presence

TABLE 3. Late Pleistocene chondrichthyans and actinopterygians from eastern Chatham County, Georgia. NISP, number of identifiable specimens; uncat., uncatalogued. Museum catalogue number of representative voucher specimen listed for each taxon. Identifications are to the lowest possible level considering the completeness of available specimens.

	Isle of	f Hope	May	fiar Site
	NISP	GSM #	NISP	GSM #
Ginglymostoma cirratum	1	568		
Carcharias taurus	3	267	12	5
Galeocerdo cuvier	2 8	269	1	788
Carcharhinus leucas		571	5	789
Carcharhinus obscurus ¹	3	574	3	
Carcharhinus sp.	23	572	9	
Negaprion brevirostris	34	575	14	790
Rhizoprionodon terraenovae	201	576	2	791
Sphyrna tiburo	32	577		
Dasyatidae	191	561		
Aetobatus narinari	1	271	4	792
Myliobatidae	67	562	34	
Lepisosteus sp.	20	615	2	794
Elops saurus	2	618		
Muraenidae	27	619		
cf. Alosa sp.	1	654		
Clupeidae	14	620		
Arius felis	2	621		
Synodus sp.	3	623	1	797
Ópsanus sp.	13	629		
Batrachoididae	7	624		
Fundulus sp. or spp.	107	631		
Prionotus sp.	6	643	7	795
Trichiurus sp.	32	640		
Lagodon rhomboides	13	644		
Archosargus probatocephalus	9	645		
Bairdiella sp., cf. B. chrysoura	10	647		
Pogonias cromis	23	649	1	799
Scianops ocellata			5	800
Mugil sp.	4	650		
Sphyraena sp.	34	652		
Bothidae	9	653		
Balistes sp.	1	655		
Lactophrys sp.	1	656		
cf. Scombridae	-		1	807
Tetraodontidae	1	657	-	
Diodontidae	6	658		
Unidentified Actinopterygii	~500	uncat.	45	uncat.

¹Or possibly Carcharhinus acronotus.

of *Lepisosteus osseus* in salt water off the modern Georgia coast. Taken together, the great abundance of marine fish and mollusks (Table 2) at the Isle of Hope, Mayfair, and Jones Girls sites is the strongest evidence that the primary depositional environment was marine, despite the presence of some terrestrial specimens. The absence of known pre-Pleistocene species at these sites indicates that no reworked Tertiary fossils are present.

Some of the records reported in Table 3 are unusual or uncommon. The identification of the extant species of nurse shark, *Ginglymostoma cirratum*, was determined by the low number of lateral crownlets on the tooth (Fig. 2A) when compared with the Tertiary species *Ginglymostoma serra*. The great numbers of teeth of the sharpnose shark, *Rhizoprionodon terraenovae* and stingrays (Dasyatidae) at the Isle of Hope Site are a function of the large amount of matrix screen-washed to recover the remains of small mammals and reptiles. *Sphyrna tiburo* is a small hammerhead shark that today is seasonally abundant in coastal and littoral waters of the southeastern United States as far north as North Carolina, but has not been reported as a fossil from this region. Its identification is based on the diagnostic posterior lower teeth, which lack a distinct cusp or cutting edge and consist of an elongate root with a thick cap of enamel (Fig.

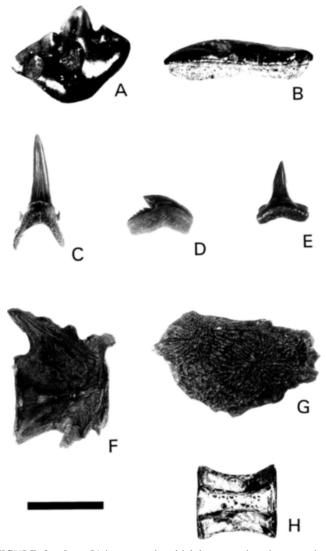


FIGURE 2. Late Pleistocene chondrichthyans and actinopterygians from Chatham County, Georgia. A-E and H from the Isle of Hope Site; F-G from Mayfair Site. A, GSM 568, tooth of *Ginglymostoma cirratum.* B, GSM 577, tooth of *Sphyrna tiburo.* C, GSM 331, tooth of *Carcharias taurus.* D, GSM 570, tooth of *Galeocerdo cuvier.* E, GSM 270, tooth of *Negaprion brevirostris.* F, GSM 800, vertebra of *Sciaenops ocellata.* G, GSM 795, dorsal view of skull cap of *Prionotus* sp. H, GSM 623, vertebra of *Synodus* sp. Scale bar = 3 mm for A-B; 20 mm for C-G; and 4.2 mm for H.

2B). One or more species of the killifish *Fundulus* are the most abundant actinopterygians in the Isle of Hope fauna. The pharyngeal and quadrate elements most closely resemble those of *Fundulus heteroclitus*. Other abundant fish in the fauna, such as the barracuda *Sphyraena*, the cutlassfish *Trichiurus*, the pinfish *Lagodon*, and the sheepshead *Archosargus*, were identified on the basis of their diagnostic teeth. Figure 2 shows representative fish elements from the two Pleistocene faunas listed in Table 3.

The Isle of Hope Site is the only Pleistocene locality in the Savannah Region to produce amphibians (Table 4), although not in especially great numbers. Only the highly aquatic genera *Siren* and *Amphiuma* are common. The tentative assignment of the Isle of Hope *Siren* to *S. intermedia* rather than *S. lacertina* is based on size, although there is some overlap in the size range of the two species (Ashton and Ashton, 1988). To date,

		Isle of Hope	e Site	Mayfair Site			
	NISP	GSM #	Diagnostic element	NISP	GSM #	Diagnostic element	
Siren sp., cf. S. intermedia	8	335	vertebra			·····	
Notophthalmus viridescens	4	549	vertebra				
Amphiuma means	15	526	dentary				
Ambystoma sp., cf. A. maculatum	1	548	vertebra				
Bufo sp.	1	553	ilium				
Pseudacris ornata	1	554	ilium				
Rana catesbeiana	2	555	articular				
Chelydra serpentina	2	274	nuchal	3	759	peripheral	
Kinosternon sp.	10	226	nuchal	1	763	nuchal	
Sternotherus sp.	3	598	plastron	1	764	hyoplastron	
Kinosternidae	60	225	misc	10	uncat.	J - F	
Apalone ferox				4	762	hyohypoplastron	
Terrapene carolina	40	314	nuchal	13	769	carapace	
Deirochelys reticularia	3	276	neural	3	765	neural	
Pseudemys sp., cf. P. concinna	11	316	peripheral				
Trachemys scripta				16	770	nuchal	
Gopherus polyphemus	2	281	costal				
Hesperotestudo incisa	7	279	epiplastron	4	786	epiplastron	
Hesperotestudo crassiscutata	2	614	shell size				
Coluber constrictor	5	580	vertebra				
Pituophis melanoleucas	2	307	vertebra				
Nerodia fasciata	2	589	vertebra				
Regina sp.	1	591	vertebra				
Thamnophis sirtalis	2	587	vertebra				
Heterodon sp.	1	585	vertebra				
Agkistrodon piscivorus	4	593	vertebra				
Crotalus sp.	4	592	vertebra				
Serpentes	50	uncat.	vertebrae	6	uncat.	vertebrae	
Alligator mississippiensis	2	282	osteoderm	8	756	osteoderm	

TABLE 4. Late Pleistocene amphibians and reptiles from eastern Chatham County, Georgia. NISP, number of identifiable specimens; uncat., uncatalogued. Museum catalog number of representative voucher specimens and diagnostic elements listed for each taxon. Identifications are to the lowest possible level considering the completeness of available specimens.

only the larger *S. lacertina* has been reported as a fossil (Holman, 1995). All but one of the amphibian species in the Isle of Hope fauna live today in coastal Georgia. A single vertebra (Fig. 3A) possesses the diagnostic characteristic of the spotted salamander, *Ambystoma maculatum*, the posterior extension of the zygapophyses beyond the neural arch (Tihen, 1958). Currently, this species is more northern in its distribution. Based on the limited number of specimens, this identification is tentative and additional specimens may show that in fact the species present is *Ambystoma tigrinum*, which is currently found along the Georgia coast. However, given that a number of the mammals in this fauna have more northern modern distributions, the presence of the spotted salamander would not be particularly unusual.

Isolated turtle carapace and plastron elements are the most common reptilian fossils at both the Isle of Hope and Mayfair sites. Emydids and kinosternids are particularly abundant (Table 4). One difference between the two faunas is that the Isle of Hope Site has the large emydid Pseudemys, while the Mayfair Site has Trachemys scripta instead. All the specimens of Terrapene represent a very large box turtle, much larger than individuals presently living in the region (Fig. 3D). Coastal Pleistocene box turtles of large size are sometimes referred to an extinct subspecies, T. carolina putnami (Auffenberg, 1958; Holman, 1995). Identification of the chicken turtle, Deirochelys reticularia, was based on the relatively wide neurals (Fig. 3C), ventral location of rib junctures on the costals, and sculpturing pattern of carapacial elements (Jackson, 1978). This is the first record of the species as a fossil outside of Florida, although its present range includes coastal Georgia.

In addition to the extant gopher tortoise, two extinct species of tortoises were present in the late Pleistocene of the southeastern Coastal Plain (Auffenberg, 1963; Holman, 1995), the relatively small *Hesperotestudo incisa* and the giant *Hesperotestudo crassiscutata*. All three are apparently present in the Isle of Hope fauna, although *H. crassiscutata* is only represented by fragmentary specimens. Both the Mayfair and Isle of Hope sites produced specimens of the diagnostic, relatively thick epiplastron of *H. incisa* (Fig. 3E–F). An incomplete plastron element of a large *Hesperotestudo* was also recovered from the Porters Pit Site (GSM 128). It could represent the Pleistocene *H. crassiscutata* or the Mio–Pliocene *H. hayi*. Use of the generic name *Hesperotestudo* rather than *Geochelone* for these species follows Preston (1979) and Meylan (1995). The presence of tortoises at Pleistocene sites is usually considered an indicator of higher winter minimum temperatures than at present.

Nine taxa of snakes have been identified from the Isle of Hope Site on the basis of vertebrae (Table 4). None are particularly abundant (relative to chelonians, fish, or even salamanders), and all are common taxa now living in coastal Georgia. The four vertebrae referred to Agkistrodon piscivorous have deep pits located lateral to the cotyle, a characteristic feature of that species (Holman, 1963, 1967). The remaining four viperid vertebrae lack these deep pits, and more resemble those of large species of Crotalus, such as C. adamanteus. The neural spines and hyapophyses are broken on all four specimens, limiting specific identification (although C. adamanteus would be expected on the basis of its modern geographic distribution). Meylan (1982:59) stated that Holman's character was subject to intracolumnar variation, with pits present on some vertebrae of C. adamanteus, but that their presence/absence would correctly identify a majority of specimens. The snake vertebra from the Jones Girls Site (GSM 821) belongs to a mediumsized natricine, but is too poorly preserved for more precise

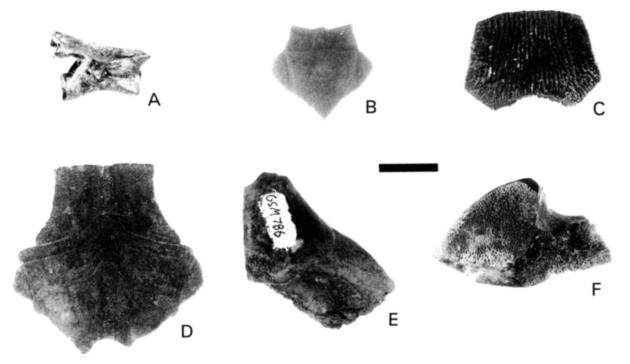


FIGURE 3. Late Pleistocene amphibian and turtles from Chatham County, Georgia. A-B from the Isle of Hope Site; C-F from Mayfair Site. A, GSM 548, lateral view of vertebra of *Ambystoma* sp., cf. A. maculatum. B, GSM 227, dorsal view of nuchal element of *Kinosternon* sp. C, GSM 765, dorsal view of neural element of *Deirochelys reticularia*. D, GSM 768, dorsal view of nuchal element of *Terrepene carolina*. E, dorsal, and F, medial views of GSM 786, right epiplastron of *Hesperotestudo incisa*. Scale bar = 2.3 mm for A; 10 mm for B; and 15 mm for C-F.

identification. Fossils of *Alligator mississippiensis* are surprisingly uncommon at the Isle of Hope Site.

Avian fossils are relatively rare in our coastal Chatham County Pleistocene sites, with only five specimens representing four taxa. A single specimen, an incomplete coracoid (GSM 612), is known from the Isle of Hope Site. It is from either *Anas rubripes* or *Anas platyrhinchos*, but its fragmentary nature prevents more exact identification. The remaining bird fossils are from the Mayfair Site and comprise the distal tarsometatarsus of *Meleagris gallopavo* (GSM 819), an incomplete coracoid of *Cygnus columbianus* (GSM 820), and two coracoids of *Anas americana* (GSM 817–818). All of these taxa are widely distributed and known today from coastal Georgia.

MAMMALIAN PLEISTOCENE VERTEBRATES FROM THE SAVANNAH REGION

In this section, we document each identifiable mammalian fossil from the Isle of Hope, Mayfair, and Porters Pit sites. This will include a listing of referred specimens, morphologic description (where necessary), and discussions regarding modern and Pleistocene distributions for each taxon.

> Infraclass MARSUPIALIA Order DIDELPHIMORPHIA Family DIDELPHIDAE

DIDELPHIS VIRGINIANA Kerr, 1792

Referred Specimens—Isle of Hope: GSM 557, fragment of left mandible, including parts of the articular condyle and inflected angle; 560, talonid of left lower molar.

Remarks—Although very incomplete, GSM 557 preserves diagnostic regions of the posterior region of the dentary, and thus can be unequivocally identified. *Didelphis virginiana* was first reported from the late Pleistocene of Georgia from Ladds

Quarry (Ray, 1967). The species remains common along the Georgia Coastal Plain today.

Infraclass Eutheria Superorder Xenarthra Order Cingulata Family Dasypodidae

DASYPUS BELLUS (Simpson), 1930

Referred Specimens—Isle of Hope: GSM 286, left metatarsal 2; 213, 214, 223, 224, 261–264, 283–285, and 607–609, approximately 135 isolated osteoderms. Mayfair: GSM 766–769, 4 osteoderms.

Remarks—The extinct armadillo, Dasypus bellus, is represented by more identifiable elements than any other mammal at the Isle of Hope Site. A wide variety of carapacial and caudal osteoderms were recovered, although all from the imbricating region of the carapace are broken. Size of the imbricating osteoderms falls within the observed range of Rancholabrean D. bellus and is much larger than in the extant D. novemcinctus (Klippel and Parmalee, 1984:fig. 3). Sample statistics are mean osteoderm maximum width, 11.8 (N = 13, s = 1.19, OR = 9.6–13.7); mean osteoderm maximum thickness, 5.7 (N = 13; s = 0.69; OR = 3.8-6.5). The second metatarsal (GSM 286) is more robust than that of UF 135645, an Irvingtonian specimen from central Florida, and more similar to that of a Rancholabrean individual, UF 16375. For example, maximum proximal width is 10.2 for UF 135645, 11.4 for UF 16375, and 11.8 for GSM 286. Martin (1974) and Downing and White (1995) noted an evolutionary trend for increasing size and robustness in this species through time.

This is only the second record of *D. bellus* from the Coastal Plain of Georgia. Klippel and Parmalee (1984) summarized the Pleistocene distribution of the species and listed records from northern Georgia and coastal regions of Florida, South Caroli-

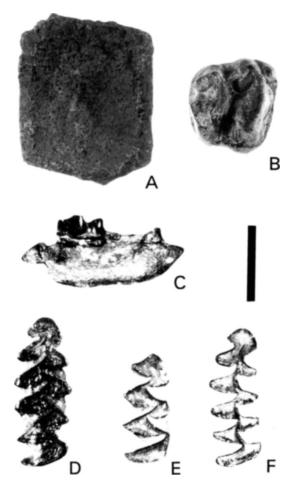


FIGURE 4. Late Pleistocene mammals from Chatham County, Georgia. C-F from the Isle of Hope Site; A-B from Mayfair Site. A, GSM 725, external view of buckler osteoderm of *Holmesina septentrionalis*. B, GSM 749, occlusal view of right M3 of *Tapirus veroensis*. C, GSM 504, lateral view of left dentary with m2 of *Blarina brevicauda*. D, GSM 432, occlusal view of right m1 of *Neofiber alleni*. E, GSM 483, occlusal view of right m1 of *Synaptomys australis*. F, GSM 430, occlusal view of right m1 of *Microtus pennsylvanicus*. Scale bar = 20 mm for A-B; 2.2 mm for C; 2.5 mm for D-E; and 2 mm for F.

na, and North Carolina. However, they overlooked Ray's (1979) report of *D. bellus* from Watkins Quarry in Glynn County, Georgia (Fig. 1).

Family PAMPATHERIIDAE

HOLMESINA SEPTENTRIONALIS (Leidy), 1889

Referred Specimens—Mayfair: GSM 725, buckler osteoderm; GSM 4, caudal osteoderm.

Remarks—The morphology of the osteoderms conforms to those of Rancholabrean *Holmesina* from Texas and Florida (James, 1957; Hulbert and Morgan, 1993). The width and thickness of GSM 725 (Fig. 4A) are 34.8 and 12.4, respectively. Only Rancholabrean specimens attain such dimensions among Florida samples (Hulbert and Morgan, 1993). *Holmesina* was first recorded from coastal Georgia, in the Brunswick region, by Frey et al. (1975), but was not previously known from the Savannah area.

Order Pilosa Family Megatheriidae

EREMOTHERIUM LAURILLARDI (Lund), 1842

Referred Specimens—Isle of Hope: GSM 202, left metacarpal 3; 210, right metacarpal 3; 409, left scaphoid; 258, left metacarpal-carpal complex; 22, incomplete ungual phalanx, probably from digit 4 of manus; 204, incomplete distal articular condyle of humerus; 203, incomplete vertebra; 205–211, 610, fragments of teeth. Porters Pit: GSM 155, tooth fragment.

Remarks—The scaphoid and metacarpal-carpal complex (MCC) match the descriptions by De Iuliis and Cartelle (1993) of these elements in *Eremotherium laurillardi* (see Cartelle and De Iuliis [1995] for nomenclature). The MCC bears a facet for a vestigial phalanx of digit 2, like ROM 22135 from the Daytona Bone Bed of Florida (De Iuliis and Cartelle, 1993:fig. 6). The third metacarpals are very robust: on GSM 202, the length from the posterior edge of the magnum facet on the proximal end to the distal articular surface is 146; anteroposterior breadth of the distal articular surface is 116.

GSM 201, 202, 258, and 409 could represent an associated individual, as they are similarly preserved and of corresponding size. This is the only such instance of possible association at the Isle of Hope Site. E. laurillardi is the numerically dominant ground sloth at all known Pleistocene coastal sites in Georgia. Georgia specimens collected in the nineteenth century were most recently listed by Cartelle and De Iuliis (1995:837). They suggested that all large, late Pleistocene species of Eremotherium, including the widely recognized E. mirabile, E. rusconii, and E. laurillardi, be synonymized, with E. laurillardi (from Brazil) having priority. Cartelle and De Iuliis (1995) stated that if their synonymy was not accepted, then Eremotherium couperi (Harlan), 1842 should have priority over E. mirabile (Leidy), 1855 for North American Rancholabrean Eremotherium. The holotype of the former was originally thought to be the femur of a sea turtle, but it later proved to be the clavicle of a megathere (Ray, 1979). Both species were named on the basis of specimens from Georgia, E. couperi from the Brunswick region and E. mirabile from the Fossilossa Site, Skidaway Island (Fig. 1).

Family MYLODONTIDAE

PARAMYLODON HARLANI (Owen), 1840

Referred Specimens—Isle of Hope: GSM 212, fragment of molariform tooth; 260, centrum of thoracic vertebra; 259, four dermal ossicles.

Remarks—GSM 212, although fragmentary and lacking any part of the occlusal surface, is complete enough to show the lobate shape diagnostic of mylodont sloths, and that it could not be derived from the structurally dissimilar teeth of *Eremotherium*. Additional evidence for a second, smaller ground sloth taxon at the Isle of Hope Site is provided by the dermal ossicles and the size of the vertebra. GSM 260 is ca. 61 mm tall and ca. 69 mm wide at its anterior articular surface. Lobate teeth and dermal ossicles are limited to *Paramylodon harlani* among Rancholabrean North American ground sloths (Kurtén and Anderson, 1980). The use of *Paramylodon* rather than *Glossotherium* follows McDonald (1995). A third genus of ground sloth, *Megalonyx*, has been reported from the Savannah area (Lipps et al., 1988), but remains of this taxon were not recovered at any of our four sites.

> Superorder Epitheria Grandorder Lipotyphla Order Soricomorpha Family Soricidae

BLARINA BREVICAUDA (Say), 1823

Referred Specimens—Isle of Hope: GSM 516, left I1; 508, 509, two left M2; 504, left mandible with m2 (Fig. 4C); 510,

TABLE 5. Measurements of the teeth of modern and fossil *Blarina*, contrasting those of *Blarina brevicauda* and *Blarina carolinensis*. Samples of modern specimens from GSM Mammalogy Collection; fossil specimens from the Isle of Hope Site, Chatham County, Georgia, are listed individually by their catalogue number in the GSM Vertebrate Paleontology Collection. "Bb" following the catalogue number of a fossil tooth indicates an assignment to *B. brevicauda*; "Bc" an assignment to *B. carolinensis*. Abbreviations: N, sample size; OR, observed range; \bar{x} , sample mean; and s, sample standard deviation.

			Labia	l length		Lingua	al length	ı	Anteri	or widt	h	Posteri	or widt	h
Species	Tooth	Ν	OR	x	s	OR	x	s	OR	x	s	OR	x	s
B. brevicauda	M1	6	1.76-1.97	1.82	0.08	1.58-1.73	1.66	0.06	1.43-1.72	1.54	0.12	1.71-2.08	1.80	0.09
B. brevicauda	M2	6	1.33-1.58	1.43	0.09	1.30-1.44	1.37	0.06	1.44 - 1.82	1.61	0.15	1.36-1.66	1.51	0.12
GSM 508 Bb	M2			1.44			1.34			1.82			1.49	
GSM 509 Bb	M2			1.41			1.42			1.69			1.27	
B. carolinensis	M1	5	1.66-1.76	1.73	0.04	1.38-1.66	1.53	0.10	1.31-1.44	1.35	0.05	1.51 - 1.78	1.66	0.10
B. carolinensis	M2	5	1.28-1.46	1.34	0.08	1.21-1.30	1.26	0.03	1.43–1.63	1.48	0.10	1.29–1.47	1.39	0.07
			AntPo	st. leng	th	Trigon	id lengt	h	Trigor	id widt	h	Talon	id widtł	ı
Species	Tooth	Ν	OR	x	s	OR	x	s	OR	x	s	OR	x	s
B. brevicauda	m1	5	1.77-1.85	1.83	0.03	0.90-1.02	0.95	0.05	0.56-0.69	0.62	0.05	1.01-1.21	1.09	0.08
GSM 505 Bb	m1			2.04			1.08			0.67			1.16	
GSM 506 Bb	m1			1.93			1.01			0.63			1.02	
B. brevicauda	m2	5	1.51-1.65	1.55	0.06	0.80-0.87	0.85	0.03	0.54-0.69	0.64	0.06	0.80-1.09	0.95	0.11
GSM 504 Bb	m2			1.53			0.80			0.69			0.79	
B. carolinensis	ml	5	1.62-1.82	1.69	0.09	0.91-1.00	0.95	0.04	0.53-0.73	0.65	0.09	0.91-1.08	0.99	0.07
B. carolinensis	m2	5	1.33-1.48	1.39	0.06	0.65-0.81	0.74	0.06	0.53-0.69	0.62	0.06	0.79-1.06	0.90	0.10
GSM 507 Bc	m2			1.48			0.74			0.76			0.92	

left edentulous mandible; 517, right il; 518, left il; 505, right m1; 506, left m1.

BLARINA CAROLINENSIS (Bachman), 1837

Referred Specimens—Isle of Hope: GSM 511, 513, two right I1; 512, 514, 515, three left I1; 503, left edentulous mandible; 507, left m2.

Remarks—There are two distinct sizes of *Blarina* present in the Isle of Hope fauna, similar to the situation seen in Ladds Quarry, Georgia (Ray, 1967; Jones et al., 1984). Table 5 shows that tooth dimensions of the larger form fall within the range of *B. brevicauda*, while the smaller specimen corresponds with *B. carolinensis*. Today, only *B. carolinensis* is known from the Georgia Coastal Plain, although both species occur in sympatry in northern Georgia and the Coastal Plain of North and South Carolina (Tate et al., 1980).

Jones et al. (1984) suggested that presence of both species at Ladds could be accounted for by heterochrony; however radiocarbon dates for various collections from the site indicate otherwise (Holman, 1985). Graham and Semken (1976) suggested that co-occurences of different species of *Blarina* in Pleistocene faunas are indicative of a more equable past climate than that of the present.

Order ERINACEOMORPHA Family TALPIDAE

SCALOPUS AQUATICUS (Linnaeus), 1758

Referred Specimen—Isle of Hope: GSM 519, right humerus.

> Grandorder FERAE Order CARNIVORA Family URSIDAE

Genus and species indeterminate

Referred Specimens—Isle of Hope: GSM 303, left lower canine: 254, proximal phalanx.

Remarks—These two specimens could belong to either *Ur*sus or *Tremarctos*, but they are inadequate to distinguish between these two ursid genera.

Family PROCYONIDAE

PROCYON LOTOR (Linnaeus), 1758

Referred Specimens—Isle of Hope: GSM 255, incomplete right mandible with p4; 256, 418, and 419, three right edentulous mandibles; 302, left mandible with p3; 257, left edentulous mandible; 423, left p4; 426, right m1; 424, left m1; 425, left m2. Mayfair: GSM 730, left edentulous mandible; 731, right m3.

Remarks—These specimens do not differ to any significant degree from modern individuals of *Procyon lotor* from coastal Georgia. The raccoon is the most abundant carnivore at the Isle of Hope Site.

Family MUSTELIDAE

LUTRA CANADENSIS (Schreber), 1776

Referred Specimen—Isle of Hope: GSM 304, incomplete left edentulous mandible.

Remarks—Identification of this specimen is based on its size, depth of the ramus, and the positions of the alveoli for the m1 and m2.

Family FELIDAE

LEOPARDUS sp.

Referred Specimen—Isle of Hope: GSM 300, right mandible with p4-m1.

Remarks—GSM 300 belongs to a small felid, close in size to the smaller members of the genus *Leopardus*, such as the margay, *L. wiedii*, and the jaguarundi, *L. yagouaroundi* (Fig. 5; Table 6). Similar specimens from the late Pleistocene of the southeastern United States have been assigned to either *Leopardus amnicola* or *L. wiedii amnicola*, depending on whether or not the fossil taxon is considered a distinct species (Gillette, 1976; Kurtén and Kaye, 1982) or a subspecies (Werdelin, 1985). GSM 300 shares various combinations of character states with each of these three taxa, but also differs from each in other features. With the limitations of having but one specimen and no indication of individual variation within the former population, the specific identification of GSM 300 remains unresolved.



FIGURE 5. Lateral (A) and lingual (B) views of GSM 350, right dentary with p4-m1 of *Lepardus* sp. from the Isle of Hope Site, Chatham County, Georgia. Ziegler Locality is a synonym for the Isle of Hope Site. Scale bar = 10 mm.

In terms of size, GSM 300 is smaller than any of the referred specimens of *L. amnicola* in eight out of sixteen characters (Table 6). Most important is the relative proportions of the p4. In *L. amnicola* and *L. wiedii*, the transverse width of the p4 is narrow relative to crown length (Gillette, 1976; Werdelin, 1985). In GSM 300, the p4 is short and broad, outside of the expected range of variation in these two taxa, and much more like that of *L. yagouaroundi*. The anterior cusplet of the p4, and, to a lesser extent, the posterior cusplet, are small and more reduced on GSM 300 than in all individuals of *L. amnicola*, *L. yagouaroundi*, and *L. wiedii* examined. Also, there is not a distinct notch between the anterior cusplet and the principle cusp of the p4 (Fig. 5A).

The ramus of GSM 300 is relatively deep anteriorly (below the diastema and the p3), as in *L. amnicola* and unlike *L. yagouaroundi* and *L. wiedii*, but it is more shallow posteriorly and more like the latter two species in this regard. The anterior margin of the ascending ramus is broad and distinct from the sharp crest forming the anterodorsal margin of the masseteric fossa (Fig. 5A). In these characters, GSM 300 closely resembles the rami of *L. amnicola* from Ladds Quarry, Ichetucknee River, and Rock Springs (Ray, 1967; Gillette, 1976), and differs from extant small *Leopardus*. The anterior margin of the coronoid rises upward steeply in *L. amnicola* and *L. yagouaroundi*, but in GSM 300 it is notably less steep, although not to the extent of *L. wiedii*. As in *L. amnicola*, GSM 300 has two large mental foramina and a relatively straight ventral border of the ramus, with only a slight convexity below the m1.

LYNX RUFUS (Schreber), 1776

Referred Specimen—Isle of Hope: GSM 301, incomplete right mandible with p3-m1.

Remarks—GSM 301 represents a larger felid than GSM 300 described in the previous section. Its p3–m1 crown length is

TABLE 6. Comparison of mandibular dimensions between GSM 300, a dentary referred to *Leopardus* sp. from the Isle of Hope Site, Chatham County, Georgia, and the observed ranges in three species of *Leopardus*: *L. amnicola*, late Pleistocene of Florida and Georgia; *L. yagouaroundi*, modern specimens; and *L. weidii*, modern specimens; all three after Gillette (1976).

	GSM 300	L. amnicola	L. yagou- aroundi	L. weidii
alveolar length, c-m1	27.6	27.3-30.4	25.4-28.1	24.7-28.3
alveolar length, p3-m1	22.4	22.9-23.8	20.1-22.6	19.4–23.9
alveolar length, p4-m1	16.5	16.7–18.1	14.5-16.7	13.9-17.2
crown length, p4-m1	16.1	16.4-18.3	14.9–16.8	14.3-17.3
p4 length	7.2	7.9-8.8	6.9-8.0	6.7-8.2
p4 width	3.6	3.4-3.9	3.3-4.1	2.7-3.6
depth of ramus at p4	16.2	16.5–19.9	15.0-18.4	14.5-16.5
m1 length	8.8	9.2–9.9	8.4–9.8	7.5–9.4
m1 width	4.0	3.8-4.8	3.5-4.2	3.1-4.0
depth of ramus at				
diastema	11.0	10.2-12.2	8.3-11.2	9.9–11.6
depth of ramus below p3	11.6	10.9-13.7	9.7-12.5	10.2-12.1
breadth of ramus at p3	5.3	4.1-6.0	4.4-5.8	4.7-5.3
depth of ramus lingual				
to p4	11.5	11.6-14.9	10.7-13.0	9.7-12.3
breadth of ramus at p4	5.6	4.3-6.5	4.7-6.0	5.0-5.9
depth of ramus at m1	11.2	11.3-14.3	10.5-12.8	10.1-12.6
breadth of ramus at m1	6.1	4.8-6.4	5.2-6.3	5.1-6.1

25.9, p4 crown length 9.0, and p4 crown width, 4.5. The size and dental morphology of GSM 301 fall within the range of variation of the extant bobcat *Lynx rufus*.

Grandorder GLIRES Order RODENTIA Family SCIURIDAE

GLAUCOMYS VOLANS (Linnaeus), 1758

Referred Specimen—Isle of Hope: GSM 500, left M1.

SCIURUS CAROLINENSIS Gmelin, 1788

Referred Specimens—Isle of Hope: GSM 822, right m1; 499, right m3.

Remarks—Both of these sciurids are common current inhabitants of the Georgia Coastal Plain. The presence of tree and flying squirrels at the Isle of Hope Site indicates that the site of deposition was not far from open woodland habitats.

Family CASTORIDAE

CASTOR CANADENSIS Kuhl, 1820

Referred Specimens—Isle of Hope: GSM 287, left M3. Mayfair: GSM 734, right P4; 735, right M2; 736, left astragalus.

Remarks—These teeth are indistinguishable from those of modern *Castor canadensis*, a species still persisting in small numbers in coastal Georgia. Although the extinct giant beaver *Castoroides* has been reported from the Brunswick region of coastal Georgia and from dredgings of the Savannah River (Cahn, 1932; Lipps et al., 1988), it has not yet been recorded from any of the low elevation sites of eastern Chatham County.

Family MURIDAE Subfamily SIGMODONTINAE

ORYZOMYS PALUSTRIS (Harlan), 1837

Referred Specimens—Isle of Hope: GSM 495, left M1; 497, left M2; 496, left m1.

SIGMODON HISPIDUS Say and Ord, 1825

Referred Specimens—Isle of Hope: GSM 523, left M1; 522, left m3.

NEOTOMA FLORIDANA (Ord), 1818

Referred Specimens—Isle of Hope: GSM 521, right M1; 520, left M2; 524, left M3; 525, incomplete lower molar.

PEROMYSCUS sp., cf. P. POLIONOTUS (Wagner), 1843

Referred Specimen—Isle of Hope: GSM 498, left m1.

Remarks—These four sigmodontine rodents are common in the southeastern United States today, and in fact are dominant members of the modern rodent fauna. Their habitat preferences range from coastal areas and sandhills (*Peromyscus polionotus*) to swampy lowlands (*Oryzomys palustris*), grasslands (*Sigmodon hispidus*), and woodlands (*Neotoma floridana*). The relatively low abundance of these rodents at the Isle of Hope Site, particularly when compared to the arvicolines, is therefore notable, and probably indicates that climatic conditions at the time of deposition were somewhat different from those of present day coastal Georgia.

Subfamily ARVICOLINAE

NEOFIBER ALLENI True, 1884

Referred Specimens—Isle of Hope: GSM 474-475, two right M1; 475, right M2; 481, 485, two left M3; 471-473, three right m1; 480, left m1; 477, 482, two right m2; 476, left m2; 473, right m3.

Remarks—These teeth from the Isle of Hope Site are smaller than those of *Ondatra zibethicus*, and the m1s and m3 possess the diagnostic features of *Neofiber alleni* (Hall, 1981:Fig. 4D). *N. alleni* presently occurs in Florida and extreme southern Georgia, where it inhabits shallow freshwater environments (Birkholtz, 1972). Late Pleistocene records of the species are known from numerous sites in Florida (Webb, 1974a), as well as Ladds Quarry and Turtle River, Georgia (Ray, 1967; Frey et al., 1975).

SYNAPTOMYS AUSTRALIS Simpson 1928

Referred Specimens—Isle of Hope: GSM 463, 467, two right M1; 484, left M1; 462, 468, two left M2; 461, 464, 483, three right m1; 466 right m2; 465, incomplete lower molar.

Remarks-These specimens are referred to Synaptomys australis on the basis of their large size (Table 7; Fig. 4E), as greater size is the primary distinguishing feature between this extinct species and the extant southern bog lemming Synaptomys cooperi (Olsen, 1958; Guilday et al., 1978; Morgan and White, 1995). S. australis is primarily known from the Rancholabrean of Florida, but there are also records from Texas, Kansas, and possibly Missouri (Webb, 1974a; Kurtén and Anderson, 1980). Ray (1967) reported two size groups of Synaptomys from Ladds Quarry, Georgia, and stated that the larger of the two was a clinal link between S. cooperi and S. australis. He also suggested that the latter was only a subspecies of the former, a hypothesis echoed by Kurtén and Anderson (1980) and, most explicitly, by Repenning and Grady (1988). More recently, Morgan and White (1995) tentatively supported the separation of the two as distinct species, based on an analysis of Irvingtonian and Rancholabrean specimens from Florida. This is the first record of S. australis north of Florida on the Atlantic Coastal Plain.

TABLE 7. Measurements of tooth length in modern and fossil specimens of the bog lemming, *Synaptomys*. Samples are: modern *Synaptomys cooperi* from the UF Mammalogy Collection (Sc-Mod); modern *S. cooperi* from Pennsylvania (Sc-PN; after Guilday et al., 1978); late Pleistocene *S. cooperi* from Robinson Cave, Tennessee (Sc-TN1; after Guilday et al., 1978); late Pleistocene *S. cooperi* from Baker Bluff Cave, Tennessee (Sc-TN2; after Guilday et al., 1978); late Pleistocene *S. cooperi* from Florida (St. Petersburg Times and Orange Lake sites), UF Vertebrate Paleontology Collection (Sa-FL1); late Pleistocene *S. australis* from Florida (Sa-FL2; after Guilday et al., 1978); and late Pleistocene *S. australis* from the Isle of Hope Site, Chatham County, Georgia (Sa-GA). Abbreviations: N, sample size; OR, observed range; \bar{x} , sample mean.

Sample	Tooth	Ν	OR	\bar{x}
Sc-Mod	M2	2	1.9-2.0	1.96
Sa-FL1	M2	2	2.5-2.6	2.55
Sa-GA	M2	2	2.4-2.5	2.42
Sc-Mod	m1	2	2.6-2.8	2.72
Sc-PN	m1	25	2.1 - 2.7	2.48
Sc-TN1	ml	71	2.3-2.9	2.65
Sc-TN2	m1	265	2.2-2.8	2.53
Sa-FL1	m1	4	3.7-4.1	3.85
Sa-FL2	m1	7	3.3-3.9	3.5
Sa-GA	m1	1	3.66	

MICROTUS (MICROTUS) PENNSYLVANICUS (Ord), 1815

Referred Specimens—Isle of Hope: GSM 469, right M3; 470, left M3; 453, right mandible with m1-m2; 429–440, 12 right m1; 441–451; 11 left m1.

Remarks—The most southern extension of the modern contiguous range of *Microtus pennsylvanicus* occurs in the Piedmont of Georgia (Golley, 1962). Disjunct, relictual populations are known as far south as Chihuahua, Mexico (Anderson and Hubbard, 1971; Martin, 1968) in the west, and in a coastal salt marsh in northern peninsular Florida in the east (Woods et al., 1982). There are numerous Pleistocene records of the species from localities south of its current range (Martin, 1968; Kurtén and Anderson, 1980), although *M. pennsylvanicus* has not previously been reported from the Pleistocene of Georgia. It is the most common rodent, and, in fact, the most common mammal (in terms of minimum numbers of individuals, 13) at the Isle of Hope Site (Fig. 4F).

MICROTUS (PITYMYS) PINETORUM (LeConte), 1830

Referred Specimens—Isle of Hope: GSM 454–457, four right m1; 458–460, three left m1.

Remarks—*Microtus (Pitymys) pinetorum* is similar in size and dental morphology to the prairie vole *M. (Pedomys) ochrogaster*, which does not occur in Georgia today. Martin (1991) reported two late Pleistocene localities in northern Georgia that contain *M. ochrogaster*, and discussed dental characters useful for distinguishing it from *M. pinetorum* (Martin, 1987, 1991). The teeth from the Isle of Hope are assigned to *M. pinetorum* using Martin's criteria. *M. pinetorum* is presently widely distributed throughout the southeastern United States, where it occurs in woodland habitats. Fossils of this species have previously been reported in Georgia from Ladds Quarry (Ray, 1967) and Kingston Saltpeter Cave (Martin, 1991), but not from the Coastal Plain.

Family HYDROCHOERIDAE

NEOCHOERUS sp., cf. N. PINCKNEYI (Hay), 1923

Referred Specimens—Mayfair: GSM 737, left i1; 738, two cheek tooth fragments. Porters Pit: GSM 153, left upper molar; 154, cheek tooth fragment.

Remarks-As discussed by Morgan and White (1995), the

systematics and nomenclature of North American fossil capybaras are presently in disarray. While certainly diagnostic to the familylevel, the limited completeness of the Georgian material does not help resolve the conflicts concerning the number of valid species and genera. We follow the traditional course of recognizing two Rancholabrean taxa, *Hydrochaeris holmesi* and *Neochoerus pinckneyi* (Kurtén and Anderson, 1980). The Mayfair and Porters Pit specimens are of moderate size, but the identification is based on the morphology of the incisor, GSM 737. It has a moderately deep groove and ridged enamel, two character states that distinguish *Neochoerus* from *Hydrochaeris* (Morgan and White, 1995). The transverse width of GSM 737 is 15.8.

Frey et al. (1975) first reported a capybara (*Hydrochaeris* sp.) from the Georgia Coastal Plain, based on a cheek tooth collected from the Turtle River (Table 1). It is unclear whether such a specimen is truly generically diagnostic. Lipps et al. (1988:135) recorded both *Hydrochaeris* (USNM 11822) and *Neochoerus* (USNM 18709, 18710) from sediments dredged out of the Savannah River. The presence of *Neochoerus* in Georgia is not surprising considering that it was previously known from both South Carolina (type locality of *N. pinckneyi*) and Florida.

Order LAGOMORPHA Family LEPORIDAE

SYLVILAGUS FLORIDANUS (Allen), 1890

Referred Specimens—Isle of Hope: GSM 486, right mandible with p3–m1; 487 and 489, two right p3s; 488, left p3; 394, left P2. Mayfair: GSM 739, lower cheek tooth.

Remarks—The Isle of Hope specimens are referred to this widespread, extant species instead of *Sylvilagus palustris* on the basis of smaller size and, on the p3, a single anterior reentrant angle and simple, thick enamel on the posterior external reentrant angle. Dimensions of the p3s are (anteroposterior length \times posterior transverse width): GSM 486, 2.0 \times 2.1; 487, 1.9 \times 1.7; and 488, 2.6 \times 2.4. The Mayfair specimen is not specifically diagnostic, but is more similar to *S. floridanus* in size.

SYLVILAGUS PALUSTRIS (Bachman), 1837

Referred Specimens—Isle of Hope: GSM 288, left mandible with p4–m3; 490, right p3; 492, left p3.

Remarks—This is the first fossil record of the marsh rabbit from Georgia. GSM 490 and 492 are larger specimens than those referred to *Sylvilagus floridanus*, and they have multiple anterior reentrant angles. Their dimensions are (anteroposterior length \times posterior transverse width): 3.7 \times 3.2 and 3.5 \times 2.9, respectively. GSM 288 lacks the diagnostic p3, but its alveolus housed a tooth even larger than GSM 490.

> Grandorder UNGULATA Order ARTIODACTYLA Family TAYASSUIDAE

MYLOHYUS FOSSILIS (Leidy), 1860

Referred Specimens—Isle of Hope: GSM 306, left M3; 305, left m3; 405, fragment of molar.

Remarks—These specimens do not differ significantly from Rancholabrean specimens of *Mylohyus fossilis* from Florida (e.g., Bader, 1957). Use of this species name follows Wright (1995), instead of *M. nasutus* as recommended by Kurtén and Anderson (1980).

Family CAMELIDAE

PALAEOLAMA MIRIFICA (Simpson), 1929

Referred Specimens—Mayfair: GSM 3, proximal phalanx; 740, right m3; 741, incomplete left m3; 742, distal metapodial.

Remarks—The teeth resemble those of *Palaeolama mirifica* and differ from those of *Hemiauchenia macrocephala* in having shorter crowns and lacking cement. Both teeth are broken, so their original lengths can not be measured, but GSM 740 has an anterior width (measured near the base of the crown) of 14.5. The proximal phalanx has a length of about 90 and a proximal articular width of 30.7.

P. mirifica is a common constituent of middle and late Pleistocene faunas in Florida (Webb, 1974b), but this is its first welldocumented occurrence in Georgia. Previous accounts of Pleistocene camelids from the state consist only of an incomplete dp4 from Ladds Quarry (Ray, 1967; its identification was equivocal, and no camelids were shown in the more recent faunal list of Holman, 1985) and an astragalus from Turtle River (Frey et al., 1975) that was described as being of the appropriate size for *P. mirifica*. Petkewich and Pratt (1989) erroneously reported a camelid from the Isle of Hope Site.

Family CERVIDAE

ODOCOILEUS VIRGINIANUS (Zimmermann), 1780

Referred Specimens—Isle of Hope: GSM 219, 220, 250, and 406, four incomplete antlers; 428, left i1; 221, 295, and 296, three upper molars; 659, right p3; 298, right m1 or m2; 297, right m3; 222, left mandibular symphysis; 249, right distal humerus; 248, right proximal ulna; 407, cervical vertebra; 266, right distal fibula; 299, proximal phalanx; 559 right naviculocuboid. Mayfair: GSM 743, right M1 or M2; 744, distal phalanx. Porters Pit: GSM 152, incomplete antler.

Remarks—In contrast to its occurrence at most Pleistocene sites in the southeastern United States, the extant *Odocoileus virginianus* is more abundant at the Isle of Hope Site than equids, camelids, tayassuids, bovids, or proboscideans. Ladds Quarry from northern Georgia is a similar exception (Ray, 1967). The fossils are not morphologically distinct from modern specimens.

Family BOVIDAE

BISON sp.

Referred Specimens—Isle of Hope: GSM 217, left P2; 216, right m3; 215, portions of a right juvenile mandible (edentulous); 247, ungual phalanx.

Remarks—The absence of horn cores make specific identification problematical (Robertson, 1974), although the intermediate size of the specimens suggests *Bison antiquus* rather than the smaller *B. bison* or the larger *B. latifrons*. The m3 has an occlusal anteroposterior length of 48.1. Pleistocene *Bison* are also known from the Fossilossa Site on Skidaway Island and the Brunswick region in coastal Georgia (Hay, 1923; Frey et al., 1975; Lipps et al., 1988).

> Order PERISSODACTYLA Family EQUIDAE

EQUUS sp.

Referred Specimens—Isle of Hope: GSM 293, partial left m1 or m2; 611, left dp3; 251, 252, and 417, three incisors; numerous uncatalogued tooth fragments. Mayfair: GSM 745, left DP2; 746, incomplete right M3; 747, left magnum; 815, left astragalus. Porters Pit: GSM 21, left P2; 149, right m3; 150, three incomplete lower check teeth.

Remarks—The limited nature of these specimens does not allow specific identification, although they represent a taxon of moderate size. GSM 21 has an occlusal anteroposterior length (apl) of 37.1 and a transverse width of 26.1 at a mesostyle crown height of 46.7. The slightly worn GSM 611 has an apl of 32.2. The heavily worn GSM 149 has an apl of 37.1.

Family TAPIRIDAE

TAPIRUS VEROENSIS Sellards, 1918

Referred Specimens—Isle of Hope: GSM 292, left DP4; 291, right p4; 290, left juvenile mandible (edentulous); 408, fragment of left juvenile maxilla. Mayfair: GSM 2, right P4; 749, right M3; 750, right p4; 751, incomplete lower molar.

Remarks—The size and morphology of the teeth match those of the well-known species *Tapirus veroensis*. For example, the anteroposterior length of GSM 291 is 21.4 and its posterior width is 18.3; for GSM 750, 21.6 and 18.6, respectively. Hulbert (1995) reported the mean and observed range (in parentheses) for these parameters in a sample of Rancholabrean *T. veroensis* p4s from Florida as 22.2 (20.8–23.7) and 20.3 (18.0–22.9), respectively (N = 14). GSM 749 (Fig. 4B) also falls well within the observed range of *T. veroensis* from Florida. It has a length of 24.5, an anterior width of 27.1, and a posterior width of 23.6. The specimens are too small to pertain to *T. haysii*, the only other recognized Pleistocene species of tapir in the eastern United States (Ray and Sanders, 1984). In Florida, the chronologic range of *T. veroensis* is late Irvingtonian through late Rancholabrean (Hulbert, 1995).

Order PROBOSCIDEA Family MAMMUTIDAE

MAMMUT AMERICANUM (Kerr), 1791

Referred Specimens—Isle of Hope: GSM 421 and 558, two cheek tooth fragments. Mayfair: GSM 753, five cheek tooth fragments. Porters Pit: GSM 20, incomplete cheek tooth; 148, cheek tooth fragment.

Remarks—These dental specimens are all fragmentary, but sufficiently complete to document the presence of the American mastodon at all three sites. Lipps et al. (1988) provided an interesting account of how a nearly complete skeleton of this species from eastern Chatham County was collected in the 1830s, and obtained by the National Museum of Natural History in Paris, France.

Family ELEPHANTIDAE

MAMMUTHUS COLUMBI (Falconer), 1857

Referred Specimens—Mayfair: GSM 754, two enamel plate fragments. Porters Pit: GSM 147, incomplete deciduous cheek tooth.

Remarks—*Mammuthus columbi* was based on a presumably late Pleistocene tooth from near Brunswick, Georgia (Hay, 1923). Most recent workers accept it as the valid name to apply to large, late Pleistocene mammoths in North America (e.g., Maglio, 1973; Agenbroad, 1984, 1994; Graham, 1986), with the exception of woolly mammoths (*M. primigenius*) from the northern United States and Canada. Kurtén and Anderson (1980) used a different scheme (following Osborn, 1922), in which *M. columbi* was applied to middle Pleistocene specimens. Mammoths are not well represented in Rancholabrean faunas from the Savannah region. The only specimen more complete than an isolated fragment of enamel is GSM 147. It consists of three and a half plates of either a third or fourth deciduous premolar and has a maximum width of 50.4. Enamel thickness is between 1.2 and 1.4.

AGE OF THE SAVANNAH REGION VERTEBRATE FAUNAS

There are at least five potential methods to determine the geologic age of Pleistocene vertebrate faunas found in the vi-

cinity of Savannah: 1) vertebrate biochronology; 2) invertebrate biochronology; 3) radioisotopic dating; 4) amino acid racemization analysis; and 5) sea-level chronology. Taken together, they support a late Pleistocene, interglacial (oxygen isotope Stage 5) age for the sites in eastern Chatham County, especially the Isle of Hope, Mayfair, and Jones Girls localities.

The vertebrate fossil fauna of the Isle of Hope Site clearly falls into the Rancholabrean Land Mammal Age (300-10 ka), and, more tentatively, the late Rancholabrean interval (130-10 ka). Bison sp., Oryzomys palustris, Sigmodon hispidus, and Synaptomys australis all made their first appearances in the southeastern United States in the Rancholabrean (Morgan and Hulbert, 1995). They provide a maximum possible age of about 300 ka. The voles Microtus pennsylvanicus and Microtus (Pitymys) pinetorum are limited to the late Rancholabrean in Florida, but both are found in older faunas elsewhere (Lundelius et al., 1987; Morgan and Hulbert, 1995). The site lacks any of the other indicators of a late Rancholabrean age, such as Puma concolor, Panthera atrox, or Dinobastis serus. These are all generally rare taxa, so their absence is not considered significant, especially at a site where large carnivores are very rare. The Isle of Hope site includes 10 taxa that became extinct by the end of the Pleistocene in North America: Eremotherium laurillardi, Paramylodon harlani, Dasypus bellus, S. australis, Tapirus veroensis, Equus sp., Mylohyus fossilis, Mammut americanum, Hesperotestudo crassiscutata, and Hesperotestudo incisa. These provide a minimum age of about 10 to 11 ka for the site. With the exception of the two species of Hesperotestudo, the remainder of the herpetofauna and the entire ichthyofauna all belong to extant taxa and do not directly provide any chronologic information other than suggesting a relatively young (Quaternary) age. Thus, on a purely chronologic basis, the vertebrate fossils of the Isle of Hope Site definitely support a Rancholabrean age, and the composition of the rodent fauna in particular is slightly more suggestive of the late rather than early Rancholabrean.

The mammalian taxa found at the Porters Pit and Mayfair sites are generally similar to those of the Isle of Hope (Table 1), but lack the diverse rodent fauna of the latter. Thus, their ages are even more poorly constrained. Their vertebrate faunas support a Rancholabrean age, but do not completely rule out the possibility of late Irvingtonian. They add four additional extinct taxa to the ten listed above for the Isle of Hope Site: *Neochoerus pinckneyi, Mammuthus columbi, Palaeolama mirifica,* and *Holmesina septentrionalis.*

There is an additional factor that may provide some chronologic information. *Eremotherium* is the numerically dominant ground sloth in the Savannah region and other coastal sites in Georgia (Hodgson, 1846; Hay, 1923; Voorhies, 1971). Florida has a much greater number of Pleistocene vertebrate sites than Georgia, with better chronologic control, thus allowing more precise resolution of the distribution of certain taxa. *Eremotherium* was common in Florida up through the last interglacial (oxygen isotope Stage 5), but thereafter became very rare and is generally absent at most sites (Morgan and Hulbert, 1995). *Megalonyx* is the typical latest Pleistocene ground sloth in Florida. Assuming that this was also the case in Georgia, abundant *Eremotherium* at sites would suggest a minimum age of about 75 ka (end of Stage 5) for these localities.

The marine/estuarine invertebrate fossil fauna recovered at the Isle of Hope Site has not been extensively studied, and separation of Pleistocene from Holocene specimens is difficult. The molluscan taxa associated with the vertebrate fossils in the Savannah region are all extant species (Table 2), and thus generally indicate a late Quaternary age (Blackwelder, 1981). More specifically, the bivalve *Anadara brasiliana* (Lamark), present at both the Isle of Hope and Jones Girls sites (Table 2), is an indicator of a late Pleistocene or younger age (Yongesian Substage of the Longian Stage) in this region (Blackwelder, 1981). Neither the ostracodes nor any other microfossils have as yet been analyzed. All but one of the molluscan species recovered still live off the Georgia coast, implying deposition when water temperatures were not significantly different from present. One gastropod from the Mayfair Site, *Melongena corona*, currently lives only to the south of the Savannah region. Thus, if contemporary with the terrestrial fossils, the invertebrate fossils provide corroborating evidence of deposition during an interglacial stage of the Pleistocene.

Two basic methods of radioisotopic dating have been widely used to determine numeric ages for late Quaternary sediments in the southeastern United States, radiocarbon and uranium-series dating. Samples of wood and peat from the Jones Girls Site were submitted for carbon-14 dating. This analysis produced an infinite date, implying an age greater than 40 ka. Almost all Useries dating in the region has been done on samples of fossil coral (Cronin et al., 1981; Szabo, 1985; Otvos, 1972 is an exception). No corals were found at the Isle of Hope Site. The poor preservation of the Pleistocene shells at this site suggests that any corals found there would not be suitable for analysis in any event. Well-preserved colonies of the stony coral Astrangia danae were recovered at the Jones Girls Site growing on dead mollusk shells. Samples were submitted to the United States Geological Survey for U-series dating and preliminary results are an age of about 80 ka (J. F. Wehmiller, pers. comm.; Wehmiller et al., 1997).

Not a single application of aminostratigraphy on Quaternary coastal sediments in Georgia was listed in the review of Wehmiller et al. (1988), although this method has been used extensively in the Carolinas and Florida. The results between aminostratigraphic and U-series age estimates are not always concordant. Not surprisingly, practitioners tend to favor the results of their own particular geochronologic method over the other (Szabo, 1985; Wehmiller et al., 1988, 1992). We did not attempt aminostratigraphic studies at the Isle of Hope Site because of the poor preservation of the shells and lack of articulated valves. Articulated valves of Mercenaria mercenaria from the Jones Girls Site were analyzed by J. F. Wehmiller; he reported their mean D/L ratio of isoleucine to be 0.63 (pers. comm. to F. Rich, 1/9/96). Similar values were obtained from the Mark Clark Pit in Charleston, South Carolina, a site that also contained corals dated in the range of 110 to 130 ka (Szabo, 1985).

The elevation of the fossil-producing strata at the Isle of Hope and Jones Girls sites (essentially at or slightly below modern sea level) and their marine ichthyofauna and mollusks together indicate that these sites were deposited during a time when relative sea level was very close (ca. -1 to +2 m) to present levels. Since sea level has been substantially lower than that during most of the late Pleistocene, this greatly constrains when deposition could have occurred. The most widely established eustatic sea level chronology for the Quaternary is derived from the study of emergent coral reefs and terraces on islands such as New Guinea, Barbados, the Bahamas, and Oahu (Bloom et al., 1974; Neumann and Moore, 1975; Bender et al., 1979). Chronologic control for these studies is provided by Useries dating and correlation with the deep sea oxygen isotope record (Shackleton and Opdyke, 1973; Aharon, 1983; Chappell and Shackleton, 1986). These strongly support the hypothesis that in the last 300,000 years (since the beginning of the Rancholabrean), sea level has only approached (or exceeded) modern values during oxygen isotope Stages 5 and 7. Correlation with any other period, for example during Stage 3, would necessitate significant tectonic uplift, on the order of 20 to 40 m, over a relatively short time frame (Szabo, 1985). This information, coupled with the mammalian and molluscan biochronology and the preliminary amino acid racemization and U-series dating results for the Jones Girls Site, is most compatible with

an interglacial, oxygen isotope Stage 5 age (ca. 125 to 75 ka) for the eastern Chatham County vertebrate sites.

PALEOECOLOGY

Of the vertebrate fossil localities located in the Savannah region, only the Isle of Hope Site has a moderately rich fauna and has been sampled in a thorough manner (particularly for microvertebrates). Therefore, our paleoecologic discussions will focus on this site. Its depositional history is complex, as a number of different environments are represented. The presence of shallow marine and intertidal mollusks and large numbers of saltwater fishes imply that deposition occurred in a nearshore marine/estuarine setting. The majority of fish species recovered from the Isle of Hope Site are most commonly found today in quiet, shallow coastal waters and estuarine habitats. Open beach and offshore habitats are poorly represented. A few taxa (e.g., Prionotus, Sphyraena, Balistes, Lactophrys) are more abundant in deeper offshore waters, but juveniles of these taxa frequent shallow bays and estuaries (Dahlberg, 1975). A small number of species are also more tolerant of low salinity waters, often on a seasonal basis (e.g., Alosa, Mugil, Fundulus). Only one taxon, Lepisosteus, is considered a true freshwater form, although individuals of this genus occur in the coastal waters of Georgia (Dahlberg, 1975). The lack of freshwater fishes indicates that input from large permanent bodies of freshwater was limited. Based on the composition of the icthyofauna, which is similar to that found in shallow marine habitats of the Georgia coast today, it is unlikely that mean water temperature at the time of deposition was significantly warmer or cooler than that of the present day. The same conclusion is indicated by the fossil mollusks.

Many of the tetrapods probably lived in close proximity to the site of deposition. Taxa known to frequent modern saltmarsh habitats include Alligator mississippiensis, Crotalus adamanteus, Dasypus novemcinctus, Blarina spp., Microtus pennsylvanicus, Oryzomys palustris, Synaptomys cooperi, Sylvilagus palustris, Procyon lotor, and Lutra canadensis (Webster et al., 1985; Frey and Pemberton, 1986). They are either present at Isle of Hope Site or are closely related to extinct species in the fauna. Taxa found at the Isle of Hope Site that are either now living on Georgia barrier islands or known to do so historically include Pituophis melanoleucas, Didelphis virginiana, Scalopus aquaticus, Odocoileus virginianus, Bison, and feral Equus (Frey and Pemberton, 1986), although all also live or lived in more upland regions. The remaining vertebrates in the Isle of Hope fauna were most likely transported from their typical habitats to the environment of deposition, probably by fluvial processes. One habitat sampled was a shallow, quiet freshwater environment. Several of the amphibian taxa, in particular the urodeles, are found today in quiet or stagnant water habitats. Other aquatic members of the herpetofauna include turtles (such as kinosternids, Pseudemys, Deirochelys, and Chelydra), natricine snakes, and the alligator. Mammalian taxa associated with primarily freshwater aquatic habitats include Neofiber alleni, Lutra canadensis, and Castor canadensis.

Upland habitats, including sandhills and woodlands, are also represented. *Peromyscus polionotus* and *Gopherus polyphemus* are common in sandhills, although in coastal Georgia *P. polionotus* also inhabits dune areas. Primarily woodland taxa include *Terrapene carolina*, *Neotoma floridana*, *Sciurus carolinensis*, *Glaucomys volans*, *Blarina carolinensis*, and *Odocoileus virginianus*. Extinct taxa presumed to be mostly woodland dwellers include *Tapirus veroensis*, *Mylohyus fossilis*, *Mammut americanum*, and *Eremotherium laurillardi*. Relatively open, grassland habitats are poorly represented at the Isle of Hope Site. Although fossils of the grazers *Bison* and *Equus* are present, they are rare in comparison to browsing ungulates.

Terrestrial climatic conditions at the time of deposition probably were not markedly different from those of the modern Coastal Plain, based on the large number of species from the Isle of Hope Site that also are found in the region today. However, there are several components of the Isle of Hope fauna that suggest the late Pleistocene climates were cooler, moister, and more equable. Of particular interest are the arvicoline rodents, which numerically dominate the rodent portion of the fauna, outnumbering sigmodontine rodents by a ratio of 6:1 (using NISP). Four arvicolines are present at the Isle of Hope Site, including three that are extralimital, Microtus pennsylvanicus, Synaptomys, and Neofiber alleni. Today, only the pine vole M. pinetorum occurs in Chatham County (Golley, 1962; Hall, 1981), and sigmodontines dominate the small mammal fauna. Graham (1976) suggested that a higher diversity of arvicolines was indicative of a cooler, moister climate with less seasonal variation in temperature. Woods et al. (1982) attributed the northward contraction of the range of M. pennsylvanicus at the end of the Pleistocene to a shift from open prairie habitats to forests in the southeastern United States. Martin (1968) proposed that a post-glacial warm-dry period may have resulted in the range restriction of this species. Like M. pennsylvanicus, Synaptomys cooperi occurs today in extreme northern Georgia, although fossil remains of this genus are found in coastal and Georgia and Florida. In contrast, the present day range of N. alleni is restricted to Florida and extreme southern Georgia. Frazier (1977) hypothesized that the range of the southern genus Neofiber contracted southward during the late Pleistocene as a result of increased aridity and decreased temperatures.

The hypothesis of a more equable Pleistocene climate than that of today on the lower Coastal Plain of Georgia is also supported by the co-occurrence of two species of Blarina, B. brevicauda, and B. carolinensis (Graham and Semken, 1976). Today the range of B. brevicauda does not extend into coastal Georgia. Modern populations of the two are sympatric in coastal marshes in Virginia and North Carolina (Webster et al., 1985). The spotted salamander, Ambystoma maculatum, is another species whose modern range does not extend south of the Georgia piedmont. However, the presence of Alligator, Dasypus, and large tortoises indicates that winter temperature minima were not significantly lower than modern conditions, and probably slightly higher. Similar "disharmonious" associations of what are today allopatric northern and southern taxa are common in late Pleistocene faunas and floras (Graham and Lundelius, 1984). Such assemblages are best explained by more equable climates with reduced seasonal extremes in temperature and greater available moisture (Graham, 1976; Graham and Lundelius, 1984). Based on all available evidence, during the last interglacial the outer Coastal Plain of Georgia was dominated by woodland and marsh habitats, and moisture and temperature regimes were not as seasonally variable as today.

CONCLUSIONS

It has been over 170 years since fossil vertebrates were first discovered in the vicinity of Savannah, but they have never before been studied faunistically. Newly discovered vertebrate sites in the region have greatly increased known faunal diversity and improved precision of chronologic interpretations. In particular, the Isle of Hope Site has produced a relatively rich fauna containing taxa of chondrichthyans, actinopterygians, amphibians, reptiles, and mammals. Its species richness far outnumbers any other known site on the Georgia Coastal Plain, and is comparable to the Ladds Quarry of northern Georgia and the diverse coastal localities of Florida.

Many of the species present are common and wide-ranging either geographically, chronologically, or both (e.g., *Mammut americanum*, *Tapirus veroensis*, and *Equus* sp.). The absence in any of the Savannah region sites of most of the large mammalian carnivores that must have been present in the area (e.g., *Canis, Smilodon, Panthera*) remains a mystery. Among the smaller carnivores, the presence of *Leopardus* is notable, especially as it appears not to be the relatively well-known, latest Pleistocene species *L. amnicola*. Their morphologic differences may be related to the older geologic age of the Isle of Hope dentary relative to most specimens of *L. amnicola*, interglacial versus latest Rancholabrean. Alternatively, it may be a true indication that a close relative of *Leopardus yagouaroundi* was at one time an inhabitant of the southeastern United States, just as there were once ocelots and margays. Only recovery of additional fossils and a better understanding of the evolutionary history of *Leopardus* will solve this problem.

A moderately diverse microvertebrate fauna from the Isle of Hope Site has been built up by screen-washing a large volume of matrix. While hardly an innovative technique at present, it has never been as successfully applied to any late Pleistocene vertebrate site on the Atlantic Coast north of Florida. Thus, many small species of fish, amphibians, snakes, and mammals are here reported from the fossil record of the Georgia Coastal Plain for the first time. The records of the environmentally sensitive urodeles, shrews, and rodents are particularly important and include some species whose modern ranges are well to the north (and west) of Savannah, such as *Blarina brevicauda*, *Microtus pennsylvanicus*, and *Ambystoma maculatum*. Others, however, have a more southerly range, such as *Neofiber alleni*.

The Pleistocene vertebrate sites of eastern Chatham County, including those from the Isle of Hope and Skidaway Island, all appear to have been deposited in association with a sea-level highstand during an interglacial interval. This is evidenced by the large numbers of marine fossils, both vertebrate and invertebrate, in these sites. However, there is at present no conclusive evidence that all the sites were contemporaneous. Detailed stratigraphic and geochronologic analysis is at present only possible for the Jones Girls Site. There vertebrate fossils were recovered from a marine shell bed that is at least 80 ka, based on amino acid racemization analysis of Mercenaria shells, radiocarbon dating of peat, and U-series dating on corals (Wehmiller et al., 1997). Multi-disciplinary geologic investigations are continuing at this locality, with the goal to correlate its strata with the nearby, original nineteenth century Fossilossa Site of Skidaway Island. The phosphatic gravel deposits in western Chatham County, such as Porters Pit, are of fluvial origin, probably were deposited during a sea-level lowstand, and contain a chronologically mixed (Miocene, Pliocene, and late Pleistocene) vertebrate fauna.

ACKNOWLEDGMENTS

We thank John Heard for his numerous contributions to our knowledge of Savannah area fossils, and the property owners of the fossil sites from which we have collected, especially the Henderson, Ziegler, and Jones families. Both Pratt and Hulbert were introduced to fossil collecting in the Savannah area by our late colleague Richard Petkewich, to whom we dedicate this report. In addition to R. Petkewich, assistance in field work and/ or helpful discussions were provided by other colleagues at Georgia Southern University (GSU), including F. R. Rich, J. D. Darrell, V. J. Henry, D. K. McLain, and S. P. Vives. Numerous GSU geology students also participated in field work or matrix processing, most notably T. Smith and M. King. S. D. Webb, D. S. Jones, R. W. Portell, M. Frank, K. Auffenberg, L. Wilkins, and D. Auth of the Florida Museum of Natural History provided access to comparative specimens. K. Seymour (ROM) provided useful comments concerning the Leopardus mandible. D. W. Steadman identified the birds and E. H. Simons the Isle of Hope actinopterygians. Helpful criticism of the manuscript was provided by JVP reviewers and editors. Funding was provided by a GSU Faculty Research Grant.

LITERATURE CITED

- Agenbroad, L. D. 1984. New World mammoth distribution; pp. 90-108 in P. S. Martin and R. G. Klein (eds.), Quaternary Extinctions, A Prehistoric Revolution. University of Arizona Press, Tucson.
- 1994. Taxonomy of North American Mammuthus and biometrics of the Hot Springs mammoths; pp. 158–207 in L. D. Agenbroad and J. I. Mead (eds.), The Hot Springs Mammoth Site: A Decade of Field and Laboratory Research in Paleontology, Geology, and Paleoecology. The Mammoth Site of Hot Springs, Hot Springs, South Dakota.
- Aharon, P. 1983. 140,000-yr isotope climatic record from raised coral reefs in New Guinea. Nature 304:720–723.
- Anderson, S., and J. P. Hubbard. 1974. Notes on geographic variation in *Microtus pennsylvanicus* in New Mexico and Chihuahua. American Museum Novitates 2460:1–8.
- Ashton, R. E., and P. S. Ashton. 1988. Handbook of Reptiles and Amphibians of Florida. Part Three: The Amphibians. Windward Publishing Inc., Miami, 191 pp.
- Auffenberg, W. 1958. Fossil turtles of the genus *Terrapene* in Florida. Bulletin of the Florida State Museum 3:53–92.
- 1963. Fossil testudine turtles of Florida, genera *Geochelone* and *Floridemys*. Bulletin of the Florida State Museum 7:53–97.
- Bader, R. S. 1957. Two Pleistocene mammalian faunas from Alachua County, Florida. Bulletin of the Florida State Museum 2:55–75.
- Bender, M. L., R. G. Fairbanks, F. W. Taylor, R. K. Matthews, J. G. Goddard, and W. S. Broecker. 1979. Uranium-series dating of the Pleistocene reef terraces of Barbados, West Indies. Geological Society of America Bulletin 90:577–594.
- Birkholtz, D. E. 1972. Neofiber alleni. Mammalian Species 15:1-4.
- Blackwelder, B. W. 1981. Late Cenozoic stages and molluscan zones of the U.S. Middle Atlantic Coastal Plain. Paleontological Society Memoir 12:1–34.
- Bloom, A. L., W. S. Broecker, J. M. A. Chappell, R. K. Matthews, and K. J. Mesolella. 1974. Quaternary sea level fluctuations on a tectonic coast: new ²³⁰Th/²³⁴U dates from the Huon Peninsula, New Guinea. Quaternary Research 4:185–205.
- Cahn, A. R. 1932. Records and distribution of the fossil beaver, Castoroides ohioensis. Journal of Mammalogy 13:229-241.
- Cartelle, C., and G. De Iuliis. 1995. *Eremotherium laurillardi*: the panamerican late Pleistocene megatheriid sloth. Journal of Vertebrate Paleontology 15:830-841.
- Chappell, J., and N. J. Shackleton. 1986. Oxygen isotopes and sea level. Nature 324:137–140.
- Cronin, T. M., B. J. Szabo, R. A. Ager, J. E. Hazel, and J. P. Owens. 1981. Quaternary climates and sea levels of the U.S. Atlantic Coastal Plain. Science 211:233–240.
- Dahlberg, M. D. 1975. Guide to the Coastal Fishes of Georgia and Nearby Shores. University of Georgia Press, Athens, 186 pp.
- De Iuliis, G., and C. Cartelle. 1993. The medial carpal and metacarpal elements of *Eremotherium* and *Megatherium* (Xenarthra: Mammalia). Journal of Vertebrate Paleontology 14:525-533.
- Downing, K. F., and R. White. 1995. The cingulates (Xenarthra) of Leisey Shell Pit 1A (Irvingtonian), Hillsborough County, Florida. Bulletin of the Florida Museum of Natural History 37:375–396.
- Frazier, M. K. 1977. New records of *Neofiber leonardi* (Rodentia, Cricetidae) and the paleoecology of the genus. Journal of Mammalogy 58:368–373.
- Frey, R. W., and S. G. Pemberton. 1986. Vertebrate Lebensspuren in intertidal and supratidal environments, Holocene barrier islands, Georgia. Senckenbergiana Maritima 18:45–95.
 - —, M. R. Voorhies, and J. D. Howard. 1975. Estuaries of the Georgia Coast, U.S.A. Sedimentology and biology VIII. Fossil and Recent skeletal remains in Georgia estuaries. Senckenbergiana Maritima 7:257–295.
- Furlow, J. W. 1969. Stratigraphy and economic geology of the eastern Chatham County phosphate district. Georgia Geological Society Bulletin 82:1–40.
- Georgia Geological Survey. 1976. Geologic Map of Georgia. Department of Natural Resources, Geology and Water Resources Division, Atlanta, 1:500,000.
- Gillette, D. D. 1976. A new species of small cat from the late Quater-

nary of southeastern United States. Journal of Mammalogy 57: 664-676.

- Golley, F. B. 1962. Mammals of Georgia. University of Georgia Press, Athens, 218 pp.
- Graham, R. W. 1976. Late Wisconsin mammal faunas and environmental gradients of the eastern United States. Paleobiology 2:343-350.
- 1986. Description of the dentitions and stylohyoids of Mammuthus columbi from the Colby Site; pp. 171–190 in G. C. Frison and L. C. Todd (eds.), The Colby Mammoth Site: Taphonomy and Archaeology of a Clovis Kill in Northern Wyoming. University of New Mexico Press, Albuquerque.
- and E. L. Lundelius. 1984. Coevolutionary disequilibrium and Pleistocene extinctions; pp. 223–249 in P. S. Martin and R. G. Klein (eds.), Quaternary Extinctions, A Prehistoric Revolution. University of Arizona Press, Tucson.
- and H. A. Semken. 1976. Paleoecological significance of the short-tailed shrew (*Blarina*), with a systematic discussion of *Blarina ozarkensis*. Journal of Mammalogy 57:433–449.
- Guilday, J. E., H. W. Hamilton, E. Anderson, and P. W. Parmalee. 1978. The Baker Bluff Cave deposit, Tennessee, and the late Pleistocene faunal gradient. Bulletin of the Carnegie Museum of Natural History 11:1-67.
- Hall, E. R. 1981. The Mammals of North America, 2nd ed. John Wiley and Sons, New York, 1181 pp.
- Hay, O. P. 1907. Description of seven new species of turtles from the Tertiary of the United States. Bulletin of the American Museum of Natural History 23:847–863.
- Henderson, S. W., and R. W. Frey. 1986. Taphonomic redistribution of mollusk shells in a tidal inlet channel, Sapelo Island, Georgia. Palaios 1:3-16.
- Henry, V. J., and J. H. Hoyt. 1965. Late Pleistocene fluvial and estuarine deposits at Savannah, Georgia. Bulletin of the Georgia Academy of Sciences 23:67-68.
- Hodgson, W. B. 1846. Memoir on the *Megatherium* and other extinct gigantic quadrupeds of the coast of Georgia with observations on its geologic features. Bartlett and Welford, New York, 47 pp.
- Holman, J. A. 1963. Late Pleistocene amphibians and reptiles of the Clear Creek and Ben Franklin local faunas of Texas. Journal of the Graduate Research Center, Southern Methodist University 31:152– 167.
- 1967. A Pleistocene herpetofauna from Ladds, Georgia. Bulletin of the Georgia Academy of Sciences 25:154–166.
- 1985. New evidence on the status of Ladds Quarry. National Geographic Research 1:569–570.
- 1995. Pleistocene Amphibians and Reptiles in North America. Oxford University Press, New York, 243 pp.
- Howard, J. D., and R. W. Frey. 1980. Holocene depositional environments of the Georgia coast and continental shelf; pp. 66–134 *in* J. D. Howard, C. B. Depratter, and R. W. Frey (eds.), Excursions in Southeastern Geology; The Archaeology-Geology of the Georgia Coast. Guidebook, 1980 Annual Meeting, Geological Society of America. Georgia Geological Survey, Atlanta.
- Hoyt, J. H., and J. R. Hails. 1974. Pleistocene stratigraphy of southeastern Georgia; pp. 192–205 in R. Q. Oaks and J. R. DuBar (eds.), Post-Miocene Stratigraphy, Central and Southern Atlantic Coastal Plain. Utah State University Press, Logan.
- Huddlestun, P. F. 1988. A revision of the lithostratigraphic units of the Coastal Plain of Georgia, the Miocene through Holocene. Bulletin of the Georgia Geological Survey 104:1-162.
- Hulbert, R. C. 1995. The giant tapir, *Tapirus haysii*, from Leisey Shell Pit 1A and other Florida Irvingtonian localities. Bulletin of the Florida Museum of Natural History 37:515–551.
- and G. S. Morgan. 1993. Quantitative and qualitative evolution in the giant armadillo *Holmesina* (Edentata: Pampatheriidae) in Florida; pp. 134–177 in R. A. Martin and A. D. Barnosky (eds.), Morphological Change in Quaternary Mammals of North America. Cambridge University Press, Cambridge.
- Hurst, V. J. 1957. Prehistoric vertebrates of the Georgia Coastal Plain. Georgia Mineral Newsletter 10:3-19.
- Jackson, D. R. 1978. Evolution and fossil record of the chicken turtle

Deirochelys, with a re-evaluation of the genus. Tulane Studies in Zoology and Botany 20:35–55.

- James, G. T. 1957. An edentate from the Pleistocene of Texas. Journal of Paleontology 31:796-808.
- Jones, C. A., J. R. Choate, and H. H. Genoways. 1984. Phylogeny and paleobiogeography of short-tailed shrews (genus *Blarina*); pp. 56– 148 in H. H. Genoways and M. R. Dawson (eds.), Contributions in Quaternary Vertebrate Paleontology: A Volume in Memorial to John E. Guilday. Carnegie Museum of Natural History, Pittsburgh.
- Klippel, W. E., and P. W. Parmalee. 1984. Armadillos in North American late Pleistocene contexts; pp. 149–160 in H. H. Genoways and M. R. Dawson (eds.), Contributions in Quaternary Vertebrate Paleontology: A Volume in Memorial to John E. Guilday. Carnegie Museum of Natural History, Pittsburgh.
- Kurtén, B., and E. Anderson. 1980. Pleistocene Mammals of North America. Columbia University Press, New York, 442 pp.
- and J. M. Kaye. 1982. Late Quaternary Carnivora from the Black Belt, Mississippi. Boreas 11:47–52.
- Leidy, J. 1855. A memoir on the extinct sloth tribe of North America. Smithsonian Contributions to Knowledge 7:1–70.
- Lipps, E. L., R. W. Purdy, and R. A. Martin. 1988. An annotated bibliography of the Pleistocene vertebrates of Georgia. Georgia Journal of Science 46:109–148.
- Lundelius, E. L., C. S. Churcher, T. Downs, C. R. Harington, E. H. Lindsay, G. E. Schultz, H. A. Semken, S. D. Webb, and R. J. Zakrzewski. 1987. The North American Quarternary sequence; pp. 211–235 in M. O. Woodburne (ed.), Cenozoic Mammals of North America, Geochronology and Biostratigraphy. University of California Press, Berkeley.
- Lyell, C. 1845. Travels in North America, in the Years 1841–2; with Geological Observations on the United States, Canada, and Nova Scotia. Volume 1. Wiley and Putnam, New York, 251 pp.
- Maglio, V. J. 1973. Origin and evolution of the Elephantidae. Transactions of the American Philosophical Society 63:1–149.
- Markewich, H. W., C. M. Hacke, and P. F. Huddlestun. 1992. Emergent Pliocene and Pleistocene sediments of southeastern Georgia: an anomalous, fossil-poor, clastic section; pp. 173–189 in C. H. Fletcher and J. F. Wehmiller (eds.), Quaternary Coasts of the United States: Marine and Lacustrine Systems. Society for Sedimentary Geology, Tulsa.
- Martin, R. A. 1968. Late Pleistocene distribution of *Microtus pennsylvanicus*. Journal of Mammalogy, 49:265-271.
- 1974. Fossil vertebrates from the Haile XIVA fauna, Alachua County; pp. 100–113 in S. D. Webb (ed.), Pleistocene Mammals of Florida. University Presses of Florida, Gainesville.

- McCartan, L., R. E. Weems, and E. M. Lemon. 1980. The Wando Formation (Upper Pleistocene) in the Charleston, South Carolina, area. United States Geological Survey Bulletin 1502-A:110–116.
- McDonald, H. G. 1995. Gravigrade xenarthrans from the early Pleistocene Leisey Shell Pit 1A, Hillsborough County, Florida. Bulletin of the Florida Museum of Natural History 37:345–373.
- Meylan, P. A. 1982. The squamate reptiles of the Inglis 1A fauna (Irvingtonian: Citrus County, Florida). Bulletin of the Florida State Museum 27:1–85.
 - 1995. Pleistocene amphibians and reptiles from the Leisey Shell Pits, Hillsborough County, Florida. Bulletin of the Florida Museum of Natural History 37:273–297.
- Milstead, W. W. 1969. Studies on the evolution of box turtles (Genus *Terrapene*). Bulletin of the Florida State Museum 14:1–113.
- Mitchell, S. L. 1824. Observations on the teeth of the *Megatherium* recently discovered in the United States. Annals of the Lyceum of Natural History of New York 1:58–61.
- Morgan, G. S., and R. C. Hulbert. 1995. Overview of the geology and vertebrate biochronology of the Leisey Shell Pit local fauna, Hills-

borough County, Florida. Bulletin of the Florida Museum of Natural History 37:1–92.

- and J. A. White. 1995. Small mammals (Insectivora, Lagomorpha, and Rodentia) from the early Pleistocene (early Irvingtonian) Leisey Shell Pit local fauna, Hillsborough County, Florida. Bulletin of the Florida Museum of Natural History 37:397–461.
- Neumann, A. C., and W. S. Moore. 1975. Sea level events and Pleistocene coral ages in the northern Bahamas. Quaternary Research 5:215–224.
- Olsen, S. J. 1958. The bog lemming from the Pleistocene of Florida. Journal of Mammalogy 39:537–540.
- Osborn, H. F. 1922. Species of American Pleistocene mammoths *Elephas jeffersonii*, new species. American Museum Novitates 41:1–16.
- Otvos, E. G. 1972. Mississippi Gulf Coast Pleistocene beach barriers and the age problem of the Atlantic-Gulf Coast "Pamlico"-"Ingleside" beach ridge system. Southeastern Geology 14:241-250.
- Petkewich, R. M., and A. E. Pratt. 1989. Pleistocene vertebrates from the Isle of Hope, Chatham County, Georgia. Georgia Journal of Science 47:21.
- Preston, R. E. 1979. Late Pleistocene cold-blooded vertebrate faunas from the mid-continental United States. I. Reptilia: Testudines, Crocodilia. Papers on Paleontology, University of Michigan Museum of Zoology 19:1–53.
- Ray, C. E. 1967. Pleistocene mammals from Ladds, Bartow County, Georgia. Bulletin of the Georgia Academy of Sciences 25:120– 150.
- 1979. Chelonia couperi Harlan 1842, a supposed turtle based on the clavicle of a megathere (Mammalia, Edentata). Notulae Naturae 455:1–16.
- and A. E. Sanders. 1984. Pleistocene tapirs in the eastern United States; pp. 283–315 in H. H. Genoways and M. R. Dawson (eds.), Contributions in Quaternary Vertebrate Paleontology: A Volume in Memorial to John E. Guilday. Carnegie Museum of Natural History, Pittsburgh.
- Repenning, C. A., and F. Grady. 1988. The microtine rodents of the Cheetah Room fauna, Hamilton Cave, West Virginia, and the spontaneous origin of *Synaptomys*. U.S. Geological Survey Bulletin 1853:1–32.
- Robertson, J. S. 1974. Fossil *Bison* of Florida; pp. 214–246 in S. D. Webb (ed.), Pleistocene Mammals of Florida. University Presses of Florida, Gainesville.
- Shackleton, N. J., and N. D. Opdyke. 1973. Oxygen isotope and palaeomagnetic stratigraphy of equatorial Pacific core V28–238: Oxygen isotope temperatures and ice volumes on a 10⁵ year and 10⁶ year scale. Quaternary Research 3:39–55.
- Szabo, B. J. 1985. Uranium-series dating of fossil corals from marine sediments of southeastern United States Atlantic Coastal Plain. Geological Society of America Bulletin 96:398–406.
- Tate, C. M., J. F. Pagels, and C. O. Handley. 1980. Distribution and systematic relationship of two kinds of short-tailed shrews (Soricidae: *Blarina*) in South Central Virginia. Proceedings of the Biological Society of Washington 93:50–60.
- Tihen, J. A. 1958. Comments of the osteology and phylogeny of ambystomatid salamanders. Bulletin of the Florida State Museum 3: 1-50.
- Voorhies, M. R. 1971. The Watkins Quarry: a new late Pleistocene mammal locality in Glynn County, Georgia. Bulletin of the Georgia Academy of Sciences 29:128.
- Webb, S. D. 1974a. Chronology of Florida Pleistocene mammals; pp. 5-31 in S. D. Webb (ed.), Pleistocene Mammals of Florida. University Presses of Florida, Gainesville.
- 1974b. Pleistocene Ilamas of Florida, with a brief review of the Lamini; pp. 170–213 in S. D. Webb (ed.), Pleistocene Mammals of Florida. University Presses of Florida, Gainesville.
- Webster, W. D., J. F. Parnell, and W. C. Biggs. 1985. Mammals of the Carolinas, Virginia, and Maryland. University of North Carolina Press, Chapel Hill, 255 pp.
- Wehmiller, J. F. D. F. Belknap, B. S. Boutin, J. E. Mirecki, S. D. Rahaim, and L. L. York. 1988. A review of the aminostratigraphy of

Quaternary mollusks from United States Atlantic Coastal Plain sites. Geological Society of America Special Paper 227:69–110.

L. L. York, D. F. Belknap, and S. W. Snyder. 1992. Theoretical correlations and lateral discontinuities in the Quaternary record of the U.S. Atlantic Coastal Plain. Quaternary Research 38:275–291.
D. E. Krantz, K. Simmons, K. R. Ludwig, H. W. Markewich, F. Rich, and R. C. Hulbert. 1997. U.S. Atlantic Coastal Plain late

- Quaternary geochronology: TIMS U-series coral dates continue to indicate 80 kyr sea level at or above present. Geological Society of America Abstracts with Program 29:A–346.
- Werdelin, L. 1985. Small Pleistocene felines of North America. Journal of Vertebrate Paleontology 5:194–210.Woods, C. A., W. Post, and C. W. Kilpatrick. 1982. *Microtus pennsyl-*
- Woods, C. A., W. Post, and C. W. Kilpatrick. 1982. Microtus pennsylvanicus (Rodentia: Muridae) in Florida: a Pleistocene relict in a coastal saltmarsh. Bulletin of the Florida State Museum 28:25–52.
- Wright, D. B. 1995. Tayassuidae of the Irvingtonian Leisey Shell Pit local fauna, Hillsborough County, Florida. Bulletin of the Florida Museum of Natural History 37:603–619.

Received 7 April 1997; accepted 9 December 1997.