

A warm thermal enclave in the Late Pleistocene of the South-eastern United States

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ABSTRACT

Physical and biological evidence supports the probable existence of an enclave of relatively warm climate located between the Southern Appalachian Mountains and the Atlantic Ocean in the United States during the Last Glacial Maximum. The region supported a mosaic of forest and prairie habitats inhabited by a “Floridian” ice-age biota. Plant and vertebrate remains suggest an ecological gradient towards Cape Hatteras (35°N) wherein forests tended to replace prairies, and browsing proboscideans tended to replace grazing proboscideans. Beyond 35°N, warm waters of the Gulf Stream were deflected towards the central Atlantic, and a cold-facies biota replaced “Floridian” biota on the Atlantic coastal plain. Because of niche diversity and relatively benign climate, biodiversity may have been greater in the south-eastern thermal enclave than in other unglaciated areas of North America. However, the impact of terminal Pleistocene megafaunal extinctions may also have been shorter and more severe in the enclave than further north. A comparison with biotic changes that occurred in North America approximately 55 million years (ma) ago at the Paleocene-Eocene Thermal Maximum suggests that similar processes of change took place under both ice-house and greenhouse climates.

Key words: Pleistocene, Wisconsinan, south-eastern U.S., climate, habitat.

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I. INTRODUCTION

The Earth is generally considered to be within an interglacial interval of a protracted ice age. A major glacial epoch ended approximately 19 millennia ago in North America, about 10 millennia after members of our species painted haunting images of ice-age mammals on cave walls in Europe (Mellars, 2006), and about 10 millennia before they began to transcribe oral epics in cuneiform in Mesopotamia (Robinson *et al.*, 2006). The approximately 11,500 years separating the height of the Last Glacial Maximum (LGM) and the end of the last advancing glacial pulse (Younger Dryas, Table 1) saw the onset of the disintegration of a huge North American continental ice cap that covered an area almost equal to that of Antarctica. Low-lying Atlantic coastal plains were flooded by rising sea levels, fed by melting glacial ice. As can readily be imagined, a profound re-organization of plant, animal and human communities accompanied gigantic patterns of change in physical environments (Anderson 2004).

We propose to review what is known of events between approximately 30,000 and 10,000 years ago, with particular reference to the biotic history of the south-eastern United States. The interval is very short relative to the average span

of existence of approximately 2.6 ma of Cenozoic terrestrial mammal species (Alroy, 2003). We will attempt to summarize current knowledge of the plant and animal communities then in existence, and to place them within a more general, continent-wide context. Our primary area of interest is the region between the crest of the Appalachian Mountains and the Atlantic Ocean, and from the southern border of Virginia to the northern border of Florida (Fig. 1). The region is noteworthy for the paucity of Pleistocene vertebrate sites it contains (see Fig. 5 in Webb *et al.* 2004). Fluvial deposits near the coast and solution cavities in limestone in more elevated areas contain remains of organisms from the late glacial and early postglacial periods. Sampling areas are dwarfed by those available to collectors in the interior of North America (see Morgan & Lucas, 2005). A few outcrops of fossil-bearing strata are exposed along the banks of gently flowing south-eastern rivers, their gradients lowered by the postglacial transgression of the Atlantic. The forests that greeted the first European colonists still blanket riverbanks, further obscuring fossil-bearing exposures. In spite of these difficulties, fossil recovery reveals the presence of a biota strikingly different from that of the 18th Century (Delcourt, 2002). Stimulated by the pioneering work of S. D. Webb (2006), we

Table 1. Late Pleistocene chronology, adapted from Mix *et al.* (2001), Anderson (2004) and Bell *et al.* (2004). Dates are approximate and are given in calendar years before the present (YBP, with “present” taken as 1950 A.D.), projected into the past from calibrated radiocarbon dates. The end of the Pleistocene (*cf.* Bell *et al.* 2004) is variously considered as: (1) the end of the major phase of megafaunal extinction in North America (12,750 y BP); (2) the end of the Younger Dryas cold event in the Northern Hemisphere (~11,570 y BP), or (3) simply rounded to 10,000 ¹⁴C yr BP (11,400 cal y BP)

Period (y BP)	Significant events	References
2,700,000	Onset of significant Northern Hemisphere glaciation	Haug <i>et al.</i> (2005)
1,770,000	Beginning of the Pleistocene	Bell <i>et al.</i> (2004)
1,350,000	<i>Mammuthus</i> appears in North America ~40 glacial cycles ago	Bell <i>et al.</i> (2004) Raymo <i>et al.</i> (2004)
210,000-160,000	Beginning of Rancholabrean Land Mammal Age, as approximated by first appearance of <i>Bison</i> south of 55°N in North America ~2 glacial cycles ago	Bell <i>et al.</i> (2004) Raymo <i>et al.</i> (2004)
130,000	Illinoian glacial interval ends, Sangamonian interglacial interval begins	Duplessy <i>et al.</i> (2007)
118,000	Wisconsinan glacial interval begins	Duplessy <i>et al.</i> (2007)
23,000-19,000	Last Glacial Maximum	Mix <i>et al.</i> (2001)
19,000	Abrupt 10 m rise in sea level due to glacial melting	Clark <i>et al.</i> (2004)
	Humans possibly present in southeastern United States	Anderson (2004)
14,500	Bølling-Allerød warming begins abruptly, onset of rapid glacial retreat, oldest credible evidence of humans in Florida, establishment of semi-permanent human settlements in Near East	Alley <i>et al.</i> (2005) Dunbar (2006) Robinson <i>et al.</i> (2006)
13,400	Clovis hunters present in mid-latitude North America	Anderson (2004)
12,800	Younger Dryas cooling abruptly begins	Alley (2000)
12,750	Extinction of megafauna essentially complete in mid-latitude North America	Webb & Simons (2006)
12,000	Beringian isthmus flooded	Keigwin <i>et al.</i> (2006)
11,570	Younger Dryas cooling abruptly ends	Alley (2000)
	Wisconsinan glacial interval ends, conventional termination of “Ice Age”	Clark <i>et al.</i> (2004)

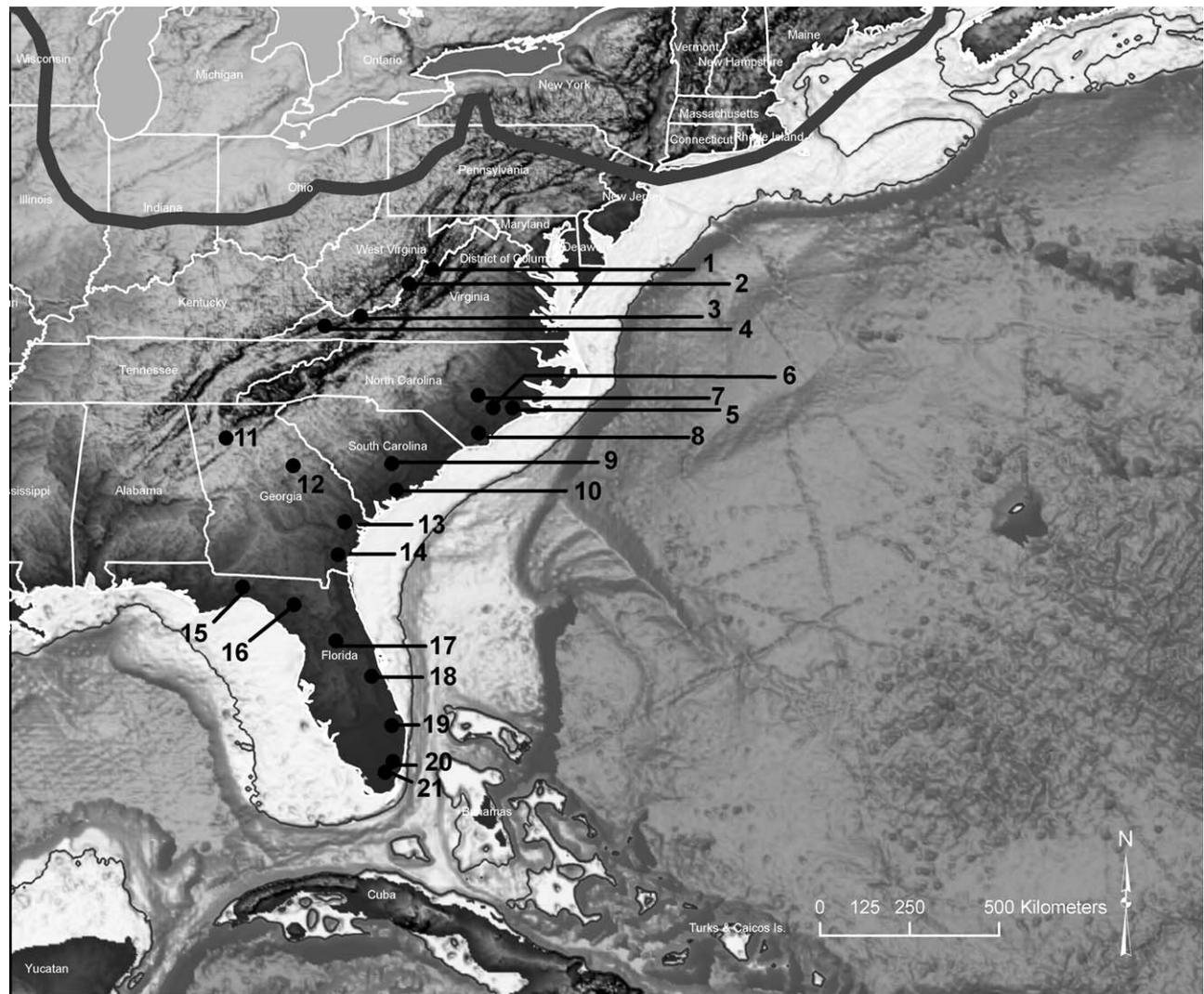


Fig. 1. Approximate limits of the 18,000 ^{14}C y BP ice margin and the -120 m isobath. The ice margin (shown as a wide grey line) crossed eastern North America in a sinuous fashion, but did not extend further south than the Ohio River and Long Island, NY. The isobath, here shown as a light line seaward of the continental shelf (shown in white, east of the US mainland), marks the presumed extent of the continental margin during the Last Glacial Maximum. The modern Atlantic Coastal Plain as well as the area shown in white could have been occupied by the terrestrial biota discussed herein. The positions of representative localities from which megafossil samples have been collected are indicated numerically. From north to south they are: for Virginia, 1, Natural Chimneys (Augusta County); 2, Strait Canyon (Highland County); 3, Early's Cave (Wythe County); and 4, Saltville (Smythe County); for North Carolina, unnamed localities are: 5, Pamlico-Carteret Counties; 6, Onslow County; 7, Duplin County; and 8, New Hanover County; for South Carolina they are: 9, Ardis (Dorchester County); and 10, Edisto Beach (Colleton County); for Georgia they are 11, Ladds Cave (Bartow County); 12, Little Kettle Creek (Wilkes County); 13, Heyner's Bridge and Skidaway Island (Chatham County); and 14, New Brunswick Channel (Glynn County); for Florida they are: 15, Page-Ladson (Jefferson County); 16, Hornsby Springs (Alachua County); 17, Rock Springs (Orange County); 18, Vero (Indian River County); 19, West Palm Beach (Palm Beach County); 20, Cutler Hammock; 21, Monkey Jungle Hammock (Dade County). See Lipps *et al.* (1988), Koch *et al.* (1998), McDonald *et al.* (1998), Hulbert (2001), Morgan (2002), Sanders (2002).

are persuaded that a fascinating period of discovery awaits investigation of the end of the ice age, as preserved in the southern mid-Atlantic states.

We maintain a regional and biological perspective, focusing on a biota that, in terms of evolutionary time, changed markedly only recently. According to a recently proposed nomenclature (based on "ecoregions," Bailey, 1998), during the late Pleistocene the south-eastern United

States apparently belonged to either a Subtropical Domain or to a hot to warm division of a Humid Temperate Domain, and was separated by a steep climatic gradient from a nearby Polar Domain. The southern part of the region is known to possess a biological cohesiveness (based on "faunal clusters," FAUNMAP 1996), and we propose that its attributes extended beyond the area where it was initially recognized. If true, this region would not have been

small. Assuming that it approximated the combined states of Florida, Georgia and the Carolinas, its area would have fallen between that of Iberia (~580,000 km²) and that originally occupied by modern coastal rainforests in the Pacific Northwest (~350,000 km²); “refugia” of temperate Pleistocene biota have been identified within both of the latter regions (Cook, Dawson, and MacDonald, 2006; Gómez & Lunt 2006; www.inforain.org). We prefer to refer to the south-eastern region informally as a relatively warm thermal enclave, bounded to the west by cooler winter temperatures and to the north by an initially stable, and then retreating, ice sheet.

II. METHODS

The present work is largely the result of a perusal of literature relevant to the biological history of the south-eastern U.S. (hereafter “Southeast”) since the LGM. The interval approximately corresponds to the late Rancholabrean (see Table 1). This North American Land Mammal Age is at present loosely calibrated by the arrival of *Bison* from Asia into mid-latitude North America between 210 and 160 thousand years (ka) ago, and the megafaunal extinctions that occurred sometime between 15 and 11.5 ka (Bell *et al.* 2004; Webb & Simons, 2006). However, most of the fossil occurrences tabulated here (see Fig. 1 for actual locations) probably date from the latter part of the Rancholabrean, extending from a brief mid-Wisconsinan glacial retreat (~30 ka; Dyke *et al.*, 2002) to the megafaunal extinction. Time is assessed by C¹⁴ dating methods, expressed in radiocarbon (¹⁴C y BP) or calendar (cal y BP) years before present. Radiometric dates are available for only a few of the many vertebrate sites that have been tabulated (see Table 3). Radiocarbon dating is only accurate to approximately 50,000 years ago (Webb *et al.*, 2004; Webb & Dunbar, 2006). Older dates were determined by radioisotopes with longer half-lives. This includes, for example, uranium-series dates from corals collected at the Jones Girls Site on Skidaway Island, Georgia (Table 3). In that case, the radioisotopes ²³⁰Th/²³⁸U were quantified to provide a date of approximately 80,000 y BP (Wehmiller *et al.*, 1997).

Floral data are from Rich (1979, 1984, 2004) and Rich *et al.* (2000), as well as from other published sources. Data from Gray’s Reef (Table 2) are presented here for the first time. Our review of vertebrate zoogeography is largely based upon published faunal lists of late Wisconsinan taxa from the southern Atlantic states, supplemented by fossil vertebrate specimens in the collections of the North Carolina Museum of Natural Sciences (NCMNS). Characterizations of vertebrate assemblages from Florida, Georgia, South Carolina, North Carolina and Virginia accompany species lists for each state (Table 3). Because the avian record is poorly sampled outside of Florida it has not been tabulated here (for avian records in Florida, see Hulbert, 2001, and Webb *et al.* 2004). The Wisconsinan vertebrate record in Florida (Hulbert, 2001; Holman, 2000, 2003) is taken as the standard for comparison with other coeval vertebrate assemblages (Table 3).

Table 2. Palynological composition of samples from Gray’s Reef. Values are expressed as per cent of total identifiable pollen and spores (minimum number of 300 grains: F. J. Rich, unpublished data)

Taxon	Gray’s Reef clay	Gray’s Reef core 1	Gray’s Reef core 2
<i>Alnus</i>	2.3	1.3	2.1
<i>Ambrosia</i>	0.89	0.97	0.62
Asteroidae	1.5	–	–
<i>Betula</i>	0.59	0.97	0.98
<i>Carya</i>	3.6	1.9	1.2
<i>Castanea</i>	0.29	1.6	0.62
Chenopodiaceae/ Amaranthaceae	15.2	8.1	5.6
<i>Corylus</i>	0.32	0.62	–
Cyperaceae	1.2	0.32	–
<i>Fagus</i>	0.59	0.32	–
<i>Fraxinus</i>	0.29	0.32	0.62
Gramineae	2.7	6.8	0.98
<i>Iva</i>	0.59	0.65	–
<i>Liquidambar</i>	1.8	–	0.30
<i>Myrica</i>	1.2	0.32	0.30
<i>Osmunda</i>	0.59	0.32	–
<i>Ostrya/Carpinus</i>	–	0.32	–
<i>Picea</i>	2.1	–	–
<i>Pinus</i>	41.7	56.5	67.2
<i>Polygonum</i>	0.59	–	–
<i>Polypodium</i>	–	0.65	–
<i>Pteridium</i>	–	0.32	–
<i>Quercus</i>	13.4	12.7	13
<i>Salix</i>	0.59	–	0.62
<i>Sambucus</i>	–	0.32	–
<i>Sphagnum</i>	0.29	0.32	–
<i>Stellaria</i>	0.29	–	–
<i>Taxodium</i>	2.1	–	0.98
<i>Tsuga</i>	0.59	–	–
<i>Ulmus</i>	0.59	0.97	0.62
<i>Woodwardia</i>	2.1	0.97	–
Indeterminate	2.1	2.6	3.7
Totals	100	100	99.4

A modified Simpson coefficient (Simpson, 1960) is here employed to assess faunal resemblance. The coefficient was originally defined as the sum of the number of species (binomial taxa) common to two assemblages, divided by the total number of recognizable species in the less diverse group. It should be noted that species lists from states north of Florida are likely to be extended significantly by future studies. The denominator is here redefined in order to compensate for uneven across-group sampling effort. Thus, rather than the total number of species in the less diverse sample, it is the sum of the species of less diverse subgroups. For example, a given list may contain 80 binomials (e.g. of mammals), including a subgroup (e.g. artiodactyls) that contains only five binomials. A second list may contain 70 mammals, including 10 artiodactyls. The lesser number of subgroup binomials is counted, in this case 5 from the less diverse subgroup in the more diverse list. The sum of subgroup counts is then divided into the number of species in common to obtain the percentage representing species “similarity.”

Table 3. Late Pleistocene vertebrate occurrences in the South-eastern United States. Generic occurrences are cited only when they document an otherwise indeterminate species. Extinct species are indicated by e and surviving species no longer living in within that state are designated as extp (extirpated)

Florida: Late Pleistocene occurrences from Florida listed by Hulbert (2001) are of late Rancholabrean age. These may include records dating to the Sangamonian interglacial but which have not been resolved by radiocarbon technology due to the effects of leaching in wet, subtropical environments (Morgan, 2002, p. 21). Floridian radiocarbon dates are listed and reviewed by Webb & Dunbar (2006). Frog occurrences are from Holman (2003). Salamander, chelonian, lizard, and mammalian occurrences are from Hulbert (2001); *Pipistrellus subflavus* is from Rabon *et al.* (2000).

Virginia: several Virginian sites (McDonald *et al.* 1998, p. 339) yielded dates, including 11,550 +/- 165 ¹⁴C y BP (Hot Run), two dates (18,780 +/- 630 and 16,830 ¹⁴C y BP) from a single tusk (Deep Creek Pit), from 27,000 to 10,050 ¹⁴C y BP (Saltville), 29,870 +/- ~1,600 ¹⁴C y BP (Strait Canyon), >36,830 ¹⁴C y BP (Virginia Beach) and >44,000 to 29,100 +/- 300 ¹⁴C y BP (Ratcliff Reservoir). Salamander, chelonian and lizard data are from Holman (1995), frogs from Holman (2003), snakes from Holman (2000), most mammalian data are from McDonald *et al.* (1998); “*Corynorhinus rafinesquii*” is from Rabon *et al.* (2000), and *Mylohyus fossilis* = *M. nasutus* is from Hulbert & Pratt (1998). For modern reptile occurrences in Virginia see Mitchell (1994).

North-west Georgia: the Ladds Quarry site has yielded dates of 10,290 +/-100 and 10,940 +/- 210 ¹⁴C y BP (Holman, 1995, p. 114), and the Kingston Saltpeter Cave 10,300 +/- 130 ¹⁴C y BP (Martin & Snead, 1989, p. 119; Holman, 1995, p. 113). Four dates from Yarbrough Cave are 14,315 +/- 755, 16,500 +/- 1,250, 18,610 +/- 960 and 23,880 +/- 200 ¹⁴C y BP (Martin, 2001, p. 33). Salamander and frog data are from Holman (1995, 2003), chelonian and lizard data are from Holman (1995), snakes are from Holman (2000), mammalian occurrences are from Ray (1967), Lipps *et al.* (1988), Rabon *et al.* (2000), Martin (2001).

Coastal Georgia: the Jones Girls Site yielded a ¹⁴C date >40,000 y BP, and U-series date of ~80,000 years. A position close to present sea level suggests a Sangamonian interglacial age (Hulbert & Pratt, 1998). The Watkins Quarry has produced seven mammal species that also occur in the Sangamon sites to the northeast, and dates averaging 10,000 ¹⁴C y BP (Voorhies, 1971; Hulbert & Pratt, 1998).

South Carolina: generic occurrences are cited only when they document an otherwise unidentified species. The Giant Cement Quarry (Dorchester County) site has been dated at 18,530 +/- 725 and 18,940 +/- 760 ¹⁴C y BP (Bentley & Knight, 1998, p. 1; Sanders, 2002, p. 10). Vertebrate occurrences are after Roth & Laerm (1980), Bentley *et al.* (1994), Bentley & Knight (1998), Holman (2000) and Sanders (2002).

South Atlantic region: the number of vertebrate species recorded simultaneously both south and north of North Carolina, and thus probably present but unrecorded in the late Pleistocene of North Carolina, includes 36 species of amphibians and reptiles, and 59 species of mammals.

North Carolina: taxonomic citations are from Hay (1923), McDonald & Ray (1989, 1993), Ray & Sanders (1984) and Sanders (2002), and collections in the North Carolina Museum of Natural Sciences.

	Florida	Virginia	North-west Georgia	Coastal Georgia	South Carolina	South Atlantic Region	North Carolina
Amphibians and reptiles							
Salamanders							
<i>Amblystoma maculatum</i> complex		X	X			X	
<i>Amblystoma</i> cf. <i>maculatum</i>				X			
<i>Amblystoma opacum</i> complex		X	X			X	
<i>Amblystoma tigrinum</i>	X	X	X			X	
<i>Amphiuma means</i>	X			X			
<i>Desmognathus fuscus</i> ?		X					
<i>Desmognathus</i> or <i>Leurognathus</i> sp.			X				
<i>Eurycea</i> sp.		X	X				
<i>Gyrinophilus porphyriticus</i>		X					
<i>Gyrinophilus</i> sp.			X				
<i>Necturus</i> sp.	X						
<i>Notophthalmus viridescens</i>	X	X	X	X		X	
<i>Plethodon glutinosus</i>	X	X	X			X	
<i>Pseudobranchius robustus</i>	X e						
<i>Pseudotriton ruber</i>			X				
<i>Pseudotriton</i> sp.		X					
<i>Siren lacertina</i>	X						
<i>Siren</i> cf. <i>S. intermedia</i>				X			
Frogs							
<i>Bufo americanus</i>		X	X			X	
<i>Bufo fowleri</i>	X	X	X			X	
<i>Bufo quercicus</i>	X						
<i>Bufo</i> sp.				X			
<i>Bufo terrestris</i>	X		X				
<i>Gastrophryne carolinensis</i>			X				
<i>Hyla chrysoscelis</i> or <i>H. versicolor</i>			X				

Table 3. (cont.)

	Florida	Virginia	North-west Georgia	Coastal Georgia	South Carolina	South Atlantic Region	North Carolina
<i>Hyla cinerea</i>	X						
<i>Hyla femoralis</i>	X						
<i>Hyla gratiosa</i>	X						
<i>Hyla squirella</i>	X						
<i>Pseudacris crucifer</i>		X	X			X	
<i>Pseudacris nigrita</i>	X						
<i>Pseudacris ornata</i>	X			X			
<i>Rana areolata</i>	X						
<i>Rana catesbeiana</i>	X	X	X	X		X	
<i>Rana clamitans</i>		X	X			X	
<i>Rana grylio</i>	X						
<i>Rana palustris</i>		X					
<i>Rana pipiens</i> complex		X extp					
<i>Rana pipiens</i>			X			X	
<i>Rana sphenoccephala</i>	X		X				
<i>Rana sylvatica</i>		X					
<i>Rana urticularia</i>			X				
<i>Scaphiopus holbrookii</i>	X	X	X				
Chelonians							
<i>Apalone ferox</i>	X			X			
<i>Apalone</i> sp.					X		
<i>Chelydra serpentina</i>	X	X		X	X	X	
<i>Chrysemys picta</i>			X		X		
<i>Clemmys guttata</i>					X		
<i>Clemmys insculpta</i>			X				
<i>Clemmys muhlenbergii</i>			X		X		
<i>Clemmys</i> sp.	X						
<i>Deirochelys reticularia</i>	X			X	X		
<i>Emydoidea blandingii</i>	X				X		
<i>Gopherus polyphemus</i>	X			X			
<i>Graptemys barbouri</i>	X						
<i>Graptemys geographica</i>		X extp					
<i>Hesperotestudo crassiscutata</i>	X e		X e	X e	X e		X e
<i>Hesperotestudo incisa</i>	X e			X e			
<i>Kinosternon bauri</i>	X						
<i>Kinosternon subrubrum</i>	X		X		X		
<i>Kinosternon</i> sp.				X			
<i>Macrochelys temminickii</i>					X		
<i>Pseudemys concinna</i>	X		X				
<i>Pseudemys</i> cf. <i>P. concinna</i>				X			
<i>Pseudemys nelsoni</i>	X		X				
<i>Pseudemys floridana</i>	X						
<i>Pseudemys</i> sp.					X		
<i>Sternotherus minor</i>	X						
<i>Sternotherus odoratus</i>	X						
<i>Sternotherus</i> sp.				X			
<i>Terrapene carolina</i>	X	X	X	X		X	
<i>Terrapene carolina putnami</i>	X e				X e		X e
<i>Trachemys scripta</i>	X			X	X		
<i>Trachemys</i> or <i>Pseudemys</i> sp.	X	X					
Lizards							
<i>Anolis carolinensis</i>	X		X				
<i>Eumeces inexpectatus</i>	X						
<i>Eumeces laticeps</i> ?		X					
<i>Eumeces fasciatus</i> ?	X						
<i>Cnemidophorus sexlineatus</i>	X						
<i>Ophisaurus ventralis</i>	X						
<i>Ophisaurus compressus</i>	X						
<i>Rhineura floridana</i>	X						

Table 3. (cont.)

	Florida	Virginia	North-west Georgia	Coastal Georgia	South Carolina	South Atlantic Region	North Carolina
<i>Sceloporus undulatus</i>	X	X	X			X	
<i>Scincella lateralis</i>		X	X			X	
Snakes							
<i>Agkistrodon contortrix</i>		X	X			X	
<i>Agkistrodon piscivorus</i>	X		X	X			
<i>Carpophis amoenus</i>	X extp	X	X			X	
<i>Cemophora coccinea</i>	X	X				X	
<i>Coluber constrictor</i>	X		X	X			
<i>Coluber</i> or <i>Masticophis</i> sp.		X			X		
<i>Crotalus adamanteus</i>	X						
<i>Crotalus horridus</i>	X	X	X			X	
<i>Crotalus</i> sp.				X			
<i>Diadophis punctatus</i>	X	X	X			X	
<i>Drymarchon corais</i>	X						
<i>Elaphe guttata</i>	X	X	X			X	
<i>Elaphe obseleta</i>	X	X	X			X	
<i>Elaphe vulpina</i>			X				
<i>Elaphe</i> sp.					X		
<i>Farancia abacura</i>	X						
<i>Heterodon platyrhinos</i>	X	X	X			X	
<i>Heterodon simus</i> ?	X						
<i>Heterodon</i> sp.				X			
<i>Lampropeltis calligaster</i>	X	X	X			X	
<i>Lampropeltis getulus</i>	X	X	X			X	
<i>Lampropeltis triangulum</i>	X	X	X			X	
<i>Masticophis flagellum</i>	X						
<i>Micrurus fluvius</i>	X						
cf. <i>Nerodia erythrogaster</i>	X						
<i>Nerodia erythrogaster</i>						X	
<i>Nerodia erythrogaster</i> ?		X					
<i>Nerodia fasciata</i>	X		X	X			
<i>Nerodia floridana</i>	X						
<i>Nerodia sipedon</i>		X	X			X	
<i>Nerodia taxispilota</i>	X						
<i>Opheodrys aestivus</i>	X	X				X	
<i>Opheodrys aestivus</i> ?			X				
<i>Opheodrys vernalis</i>		X					
<i>Pituophis melanoleucus</i>	X		X	X			
<i>Regina alleni</i>	X						
<i>Regina septemvittata</i> ?		X					
<i>Regina</i> sp.			X	X			
<i>Rhabdinaea flavilata</i>	X						
<i>Sistrurus miliaris</i>	X						
<i>Stilosoma extenuatum</i> ?	X						
<i>Storeria dekayi</i>	X	X	X			X	
<i>Storeria occipitomaculata</i>		X					
<i>Tantilla relicta</i>	X						
<i>Thamnophis sauritus</i> ?		X	X			X	
<i>Thamnophis sirtalis</i>	X	X	X	X		X	
<i>Virginia striatula</i>		X	X			X	
<i>Virginia valeriae</i>		X	X				
Crocodylians							
<i>Alligator mississippiensis</i>	X		X	X	X		X
cf. <i>Gavialosuchus</i> sp.					X		
Mammals							
Marsupials							
<i>Didelphis virginiana</i>	X	X	X	X	X	X	
Insectivores							
<i>Blarina brevicauda</i>		X	X	X		X	

Table 3. (cont.)

	Florida	Virginia	North-west Georgia	Coastal Georgia	South Carolina	South Atlantic Region	North Carolina
<i>Blarina carolinensis</i>	X		X	X			
<i>Condylura cristata</i>		X			X	X	
<i>Cryptotis parva</i>	X	X	X			X	
<i>Microsorex hoyi</i>		X					
<i>Parascalops breweri</i>		X	X				
<i>Scalopus aquaticus</i>	X	X	X	X	X	X	
<i>Sorex arcticus</i>		X extp					
<i>Sorex brevicauda</i>					X		
<i>Sorex cinereus</i>		X	X			X	
<i>Sorex dispar</i>		X					
<i>Sorex fumeus</i>		X	X			X	
<i>Sorex longirostris</i>	X						
<i>Sorex cf longirostris</i>					X		
<i>Sorex palustris</i>		X					
Bats							
“ <i>Corynorhinus</i> ” <i>rafinesquii</i>		X					
<i>Desmodus stocki</i>	X e						
<i>Eptesicus fuscus</i>	X	X	X			X	
<i>Eumops glaucinus</i>	X						
<i>Eumops underwoodi</i>	X extp						
<i>Lasiomycterus noctivagans</i>		X					
<i>Lasiurus borealis</i>	X	X				X	
<i>Lasiurus intermedius</i>	X						
<i>Lasiurus seminolus</i>	X						
<i>Mormoops megalophylla</i>	X extp						
<i>Myotis austroriparius</i>	X						
<i>Myotis grisescens</i>	X	X	X			X	
<i>Myotis keenii</i>		X					
<i>Myotis leibii</i>		X					
<i>Myotis lucifugus</i>			X				
<i>Myotis lucifugus</i> or <i>M. sodalis</i>		X					
<i>Nycticeius humeralis</i>	X						
<i>Pipistrellas subflavus</i>	X	X	X			X	
<i>Plecotus townsendii</i>		X					
<i>Pteronotus pristinus</i>	X e						
<i>Tadarida brasiliensis</i>	X						
Primates							
<i>Homo sapiens</i>	X	X				X	
Xenarthra (edentates)							
<i>Dasybus bellus</i>	X e	X e	X e	X e	X e	X e	
<i>Eremotherium laurillardi</i>	X e			X e	X e		
<i>Eremotherium</i> sp.							X e
<i>Glyptotherium floridanum</i>	X e				X e		
<i>Holmesina septentrionalis</i>	X e			X e	X e		
<i>Holmesina</i> sp.							X e
<i>Megalonyx jeffersoni</i>	X e	X e			X e	X e	
<i>Megalonyx</i> sp.			X e	X e			X e
<i>Paramylodon harlani</i>	X e			X e			
<i>Paramylodon</i> sp.					X e		
Rabbits							
<i>Lepus americanus</i>		X					
<i>Ochotona</i> spp.		X extp					
<i>Sylvilagus floridanus</i>	X	X		X	X	X	
<i>Sylvilagus transitionalis</i>		X	X			X	
<i>Sylvilagus palustris</i>	X			X	X		
<i>Sylvilagus palustrellus</i>	X e						
Rodents							
<i>Castor canadensis</i>	X	X	X	X	X	X	

Table 3. (cont.)

	Florida	Virginia	North-west Georgia	Coastal Georgia	South Carolina	South Atlantic Region	North Carolina
<i>Castoroides ohioensis</i>	X e	X e		X e	X e	X e	
<i>Castoroides</i> sp.							X
<i>Clethrionomys gapperi</i>		X					
<i>Erethizon dorsatum</i>	X extp	X			X	X	
<i>Eutamias minimus</i>		X extp					
<i>Geomys pinetis</i>	X			X			
<i>Glaucomys sabrinus</i>		X	X			X	
<i>Glaucomys volans</i>	X	X	X	X	X	X	
<i>Hydrochoerus holmesi</i>	X e			X			
<i>Hydrochoerus</i> sp.					X e		X e
<i>Marmota monax</i>		X	X			X	
<i>Microtis chrotorrhinus</i>		X					
<i>Microtis pennsylvanicus</i>	X extp	X	X	X	X	X	
<i>Microtis pinetorum</i>	X	X	X	X	X	X	
<i>Microtis xanthognathus</i>		X extp					
<i>Napaeozapus insignis</i>		X	X			X	
<i>Nechoerus pinkneyi</i>	X e			X e	X e		
<i>Neofiber alleni</i>	X		X	X	X		
<i>Neofiber leonardi</i>		X e					X
<i>Neotoma floridana</i>	X	X	X	X	X	X	
<i>Ochrotomys nuttalli</i>	X						
<i>Ondatra zibethicus</i>	X extp	X	X		X	X	
<i>Oryzomys palustris</i>	X		X	X	X		
<i>Peromyscus cumberlandensis</i>			X				
<i>Peromyscus gossypinus</i>	X	X				X	
<i>Peromyscus leucopus</i>		X				X	
<i>Peromyscus</i> cf. <i>Leucopus</i>			X				
<i>Peromyscus maniculatus</i>		X				X	
<i>Peromyscus</i> cf. <i>maniculatus</i>			X				
<i>Peromyscus polionotus</i>	X			X			
<i>Peromyscus</i> sp.					X		
<i>Phenacomys intermedius</i>		X extp					
<i>Podomys floridanus</i>	X						
<i>Reithrodontomys humulis</i>	X						
<i>Reithrodontomys fulvescens</i>	X extp						
<i>Sciurus carolinensis</i>	X	X	X	X	X	X	
<i>Sciurus niger</i>	X		X				
<i>Sigmodon hispidus</i>	X		X	X			
<i>Spermophilus tridecemlineatus</i>		X	X		X	X	
<i>Spermophilus</i> sp.	X			X			
<i>Synaptomys australis</i>	X e			X	X		
<i>Synaptomys borealis</i>		X extp					
<i>Synaptomys cooperi</i>		X	X		X	X	
<i>Tamias aristus</i>	X e		X				
<i>Tamias striatus</i>		X	X			X	
<i>Tamiasciurus hudsonius</i>		X	X			X	
<i>Thomomys orientalis</i>	X e						
<i>Zapus husonicus</i>		X	X			X	
Carnivores							
<i>Arctodus simus</i>		X e					
<i>Canis dirus</i>	X e	X e			X e	X e	
<i>Canis latrans</i>	X	X				X	
<i>Canis lupus</i>		X				X	
<i>Canis rufus</i>	X extp						
<i>Canis</i> cf. <i>lupus</i>			X				
<i>Canis</i> sp.							X
<i>Conepatus leuconotus</i>	X extp		X				
<i>Conepatus robustus</i>	X e						
<i>Conepatus</i> cf. <i>C. robustus</i>					X		

Table 3. (cont.)

	Florida	Virginia	North-west Georgia	Coastal Georgia	South Carolina	South Atlantic Region	North Carolina
<i>Dinobastis serus</i>	X e						
<i>Leopardus amnicola</i>	X e						
<i>Leopardus pardalis</i>	X extp						
<i>Leopardus</i> sp.				X extp			
<i>Lutra canadensis</i>	X		X	X	X		
<i>Lynx rufus</i>	X		X	X	X		
<i>Lynx</i> sp. indet.		X					
<i>Martes americana</i>		X extp					
<i>Martes pennanti</i>		X extp	X			X	
<i>Mephitis mephitis</i>		X	X		X	X	
<i>Mustela erminea</i>		X extp					
<i>Mustela frenata</i>	X	X				X	
<i>Mustela</i> cf. <i>frenata</i>			X				
<i>Mustela rixosa</i>		X					
<i>Mustela vison</i>	X	X			X	X	
<i>Miracinonyx trumani</i>	X e						
<i>Panthera atrox</i>	X e	X e				X e	
<i>Panthera leo atrox</i>		X e			X e		
<i>Panthera onca</i>	X extp		X extp		X extp		
<i>Procyon lotor</i>	X	X	X	X	X	X	
<i>Puma concolor</i>	X		X		X		
<i>Smilodon fatalis</i>	X e				X e		
<i>Spilogale putorius</i>	X	X	X		X	X	
<i>Tremarctos floridanus</i>	X e		X e		X e		
<i>Urocyon cinereoargenteus</i>	X	X	X			X	
<i>Urocyon</i> cf. <i>cinereoargenteus</i>					X		
Ursidae sp. indet.				X			
<i>Ursus americanus</i>	X	X	X			X	
<i>Ursus arctos</i>	X extp						
<i>Vulpes vulpes</i>		X					
<i>Vulpes</i> sp.	X						
Proboscidians							
<i>Mammot americanum</i>	X e	X e	X e	X e	X e	X e	X e
<i>Mammuthus columbi</i>	X e			X e			X e
<i>Mammuthus</i> cf. <i>columbi</i>					X e		
<i>Mammuthus primigenius</i>		X e					X e
<i>Mammuthus</i> sp.			X e				
Perissocactyls							
<i>Equus alaskae</i> group	X e						
<i>Equus complicatus</i>		X e				X e	
<i>Equus</i> cf. <i>complicatus</i>					X e		
<i>Equus (Amerhippus) fraternus</i>	X e					X e	
<i>Equus fraternus</i>		X e					
<i>Equus laurentius</i> group	X e						
<i>Equus</i> sp.			X e	X e			X e
<i>Tapirus veroensis</i>	X e	X e	X e	X e	X e	X e	X e
Artiodactyls							
<i>Alces alces</i>		X extp					
<i>Bison antiquus</i>	X e						
<i>Bison antiquus antiquus</i>					X e		
<i>Bison</i> sp.			X extp	X extp			X extp
<i>Bison</i> spp. indet.		X e					
<i>Blastocerus extraneus</i>	X e						
<i>Bootherium bombifrons</i>		X e					X e
<i>Cervalces</i> sp. indet.		X e					
<i>Cervus elaphus</i>		X extp			X extp	X extp	X extp
<i>Hemiauchenia macrocephala</i>	X e						
<i>Mylohyus fossilis</i>	X e	X e	X e	X e	X e	X e	
<i>Odocoileus virginianus</i>	X	X	X	X	X	X	

Table 3. (cont.)

	Florida	Virginia	North-west Georgia	Coastal Georgia	South Carolina	South Atlantic Region	North Carolina
<i>Odocoileus</i> sp.							X
<i>Palaeolama mirifica</i>	X e			X e	X e		
<i>Platygonus compressus</i>	X e	X e	X e			X e	
<i>Platygonus</i> sp.							X e
<i>Platygonus vetus</i>		X e					
<i>Sangamon</i> sp. indet.		X e					
<i>Rangifer tarandus</i>		X extp	X extp			X extp	

III. THE PHYSICAL ENVIRONMENT

Glaciers descended into lowlands of the Northern Hemisphere 2.7 ma ago (Haug *et al.*, 2005), and within 200 ka had coalesced into continental ice sheets. Ocean levels began to rise and fall in rhythmic response to the accumulation and melting of huge volumes of polar ice. Over the past 1.8 ma, North America has been subjected to no less than 27 glacial intervals. Between 1,200 and 600 ka ago, the glaciation-inundation couplets lengthened from 40 to 100 ka (the “Mid-Pleistocene Revolution”). Ice sheets simultaneously increased in volume and ocean levels fluctuated by 120 m (Heslop, Dekkers, and Langereis, 2002; Raymo *et al.*, 2004; Miller *et al.* 2005).

During the interglacial period antedating the present one (Sangamonian, ~130 to 118 ka ago) sea levels were 4-6 m higher than today, and summer temperatures over northern North America were 2-5°C warmer than at present. Most of North America was free of continental ice (North Greenland Ice Core Project Members, 2005; Heusser & Oppo, 2003). Climatic conditions then gradually cooled into the most recent (Wisconsinan) glacial interval (Hearty & Neumann, 2001; Duplessy, Roche, and Kageyama, 2007). After a brief warming event (Mid-Wisconsinan Interstadial, 27,000-30,000 ¹⁴C y BP), when the central North American ice sheet was confined to the Canadian Shield, an enormous sheet of ice rapidly spread over the continent. At the LGM (18,000 ¹⁴C ky BP, or 21,000 cal y BP) the sheet contained approximately 16 million km³ of ice, or about half that the Antarctic ice cap. It extended over about 12 million km², about half of North America or an area equivalent to about 85% of Antarctica (Swithinbank, 1988; Dyke *et al.*, 2002). The global accumulation of land ice produced a worldwide sea level fall of 114-135 m (Mix, Bard, and Schneider, 2001; Marshall, James, and Clarke, 2002). Casual inspection of a world atlas suggests that about 1 million km² of previously inundated continental shelf was added to the coastal lowlands of North America during the LGM. The Beringian Isthmus between Alaska and Siberia was emergent during the last glacial interval (Keigwin *et al.*, 2006; Samthein *et al.*, 2006), as it must have been during preceding glacial intervals [see discussion of mammalian immigrations in Bell *et al.* (2004), and Raymo *et al.* (2004)].

The Southern Appalachian Mountains were located slightly more than 500 km south of the LGM glacial front in Ohio (Hausen, 1997; Dyke *et al.*, 2002), among which Mount Mitchell now rises to an elevation of 2,037 m. The absence of evidence for high-altitude glaciers, and the persistence of an endemic flora on Appalachian crests today imply that the mountains were not glaciated during peak glacial intervals (McKeon *et al.*, 1974; Delcourt, 2002; Ibáñez *et al.*, 2006). How this apparently anomalous condition could exist so near a gigantic body of continental ice begs a regional explanation. This question may, in part, be sought in oceanic and atmospheric circulation patterns east of the mountains.

The Gulf Stream functioned as an oceanic heat conveyer during the late Pleistocene much as it does today. After emerging from the Florida Straits, it flows northward along the continental margin of North America until it is deflected eastward toward the open ocean at Cape Hatteras. Sea surface temperatures south of the Cape are maintained between 21 and 28°C throughout the year by warm tropical water. During full glacial periods the Gulf Stream followed the same course (Matsumoto & Lynch-Stieglitz, 2003), presumably also warming the Carolina coast. Although it was probably weaker when it emerged from the Florida Straits during glacial intervals (Lynch-Stieglitz, Spero, & Lea, 1999), the current may well have been accelerated from approximately 30 to 90 m³ s⁻¹ by wind-driven recirculation in the western North Atlantic. Thus, a weakened flow through the Florida Straits during the late Pleistocene need not imply a reduced northward flow of warm water along the eastern coast of North America.

During the late Pleistocene, the waters in the tropical North Atlantic were probably 2-4°C cooler than today (CLIMAP, 1981; Schmidt, Spero, & Lea, 2004; Trend-Staid & Prell, 2002), producing cooler Gulf Stream temperatures further north. An assemblage of planktonic foraminifera from a sediment core located at about 35°N in the western North Atlantic suggests mean annual temperatures about 2°C cooler than at present (Trend-Staid & Prell, 2002). Between 24,000 and 64,000 cal y BP, foraminiferal abundances east of the Gulf Stream (30°45'N, 74°28'W) suggest temperatures of approximately 19°C during cold intervals *versus* 21°C today and August temperatures of 23°C *versus* 28°C today (Vautravers & Shackleton, 2004). Oxygen isotope data from planktonic foraminifera support

reduced seasonality, with wintertime temperatures only slightly cooler than at present (Matsumoto & Lynch-Stieglitz, 2003). Measurements derived from surface-dwelling foraminifera (*Globigerina ruber* and *G. sacculifer*) south of the Gulf Stream imply substantial cooling during glacial intervals. These warm-tolerant foraminifera presumably calcified during the summer. The deep-dwelling foraminiferan *G. truncatulinoides*, which calcifies in waters formed in deep winter-mixed layers further north (but still south of the Gulf Stream), shows only a small difference between glacial and interglacial values. The difference can be explained by expected changes in the isotopic composition of sea-water between glacial and interglacial periods.

Relatively warm late Pleistocene winter sea surface temperatures may have moderated climates in the Carolinas south of Cape Hatteras. How far inland warming extended would have depended on the direction of prevailing winter winds. Climate models produce differing results, some suggesting prevailing winter winds from the south/south-west over the south-eastern U.S. (Dong & Valdes, 1998), and others a shift to more westerly or northerly flow (Bromwich *et al.*, 2004; Shin *et al.*, 2003). The model with the best spatial resolution (Bromwich *et al.*, 2004) suggests a severe 15°C wintertime cooling from katabatic winds sweeping over the region from the large northerly ice sheet. However, noble gas concentrations in ground waters in Georgia show only a 4°C lowering of mean annual temperature (Clark *et al.*, 1997). This is in striking contrast to the more severe cooling north of Cape Hatteras (9°C) in Maryland, also inferred from concentrations of noble gases in ground waters (Aeschbach-Hertig *et al.*, 2002).

Observations at the Wilmington Airport, North Carolina, since 1948 indicate that between February and August prevailing winds are from the south-west, and tend to blow from the north-north-east during the remainder of the year. Higher velocity storm winds (summer hurricanes and winter “nor’easters”) also tend to blow from the north-east, but are less frequent than sustained but lower velocity spring and summer winds. In either case, relatively warm oceanic air would sweep approximately 50 km across the adjacent coastal plain (Ryan Boyles, personal communication, North Carolina State Climate Office, 2005, see National Climatic Data Center, November 1998, Climatic wind data for the United States). Between the LGM and the beginning of the Holocene, and at least as far south as 40° N, isotopic evidence indicates that precipitation-bearing winds from the north-east swept across eastern North America deep into the continent (Feng *et al.*, 2007). Sedimentary patterns suggest that coastal lakes (“Carolina bays”) may have been deformed by winds blowing from the south-west (Soller & Mills, 1991). Deformation associated with some bays was active both during and after the maximum advance of the Wisconsin ice sheet. The general direction of prevailing winds has apparently been maintained parallel to a northeast-southwest axis over the last 36,000 years (Markewich & Markewich 1994; Ewing *et al.*, 2001; Zanner, Wysocki, & Vepraskas, 2002; Ivester *et al.*, 2003). Their net effect may have been consistent with the presence of a warm thermal enclave east of the Southern Appalachians

during the late Pleistocene, a possibility that merits further scrutiny.

The LGM was terminated by a post-glacial melting epoch that began with a melt-water pulse generated by the partial collapse of Northern Hemisphere ice sheets 19,000 cal y BP and ended in a stabilization of global sea levels 7,000 cal y BP. During this interval glacial waters produced a sea-level rise averaging 1 m per century. Exceptions occurred in melt-water pulses at 19,000 and 14,500 cal y BP. In both cases sea-level rise increased by a factor of five for several centuries, signaling the collapse of ice sheets in the Northern Hemisphere (Clark *et al.*, 2004, Alley *et al.*, 2005). Melting was arrested for more than a millennium during a final glacial epoch (the Younger Dryas), and ended abruptly in the major warming of 11,570 cal y BP that marks the end of the “Ice Age” interval (Alley, 2000; Lohne *et al.*, 2004). The Holocene Thermal Maximum (11,000 to 9,000 cal y BP) followed, when high-latitude temperatures averaged 1.6°C warmer than at present (PARCS Group 2004). Melt water produced an enormous glacial lake (Lake Agassiz) which attained a volume nearly double that of the modern Caspian Sea in Eurasia. When the mid-continental ice sheet disintegrated 8,500 cal y BP, a flow of water was discharged into the St. Lawrence Valley in eastern Canada that for a year equaled one-sixth that of the Gulf Stream (Clarke *et al.*, 2003). Ocean levels have since stabilized, with no significant net loss of glacial ice (Milne, Long & Bassett, 2005). During the last few decades a sea-level rise of 32 cm per century has been attributed to thermal expansion of the World Ocean rather than to melting ice (Cabanes, Cazenave & LeProvost, 2001).

During the late Pleistocene, lowland environments bordering the South Atlantic Bight extended 900 km from Cape Canaveral in the south-west to Cape Hatteras in the north-east. They harboured a physical environment not greatly different from that of Florida. The biogeographic importance of this region was further enhanced by a substantial increase in land area due to a drop in sea level, adding an area to the Bight exceeding that of the state of South Carolina. Remarkable changes have transpired in physical environments during the few tens of thousands of years separating the LGM from the beginning of the Holocene in North America. How did indigenous biota respond?

IV. THE PALAEOBOTANICAL ENVIRONMENT

(1) Change in North American plant associations during the Pleistocene

Ancient floras exhibiting a species composition unlike those of modern floras, i.e. those with mixed compositions and harbouring different spectra of species, are well documented in the Southeast (Jackson & Williams, 2004), but have not always been recognized. Early interpretations of the distribution of plant communities in the region generally held that forest types (boreal, mixed mesophytic, tropical, *etc.*) occupied distinct geographic areas (Braun, 1950; Delcourt, 2002). The South-eastern flora, as visually

described by the first Europeans, was considered to be an intact remnant of a much more ancient Tertiary flora (Whitehead, 1965; Watts, 1971). Indeed, species comprising the south-eastern evergreen forest have maintained a presence in the Southeast for a very long time.

Although plants lack the obvious mobility of animals, the rapid infilling of an open meadow by trees and shrubs provides familiar, visible evidence of their ability to alter their distributions. Movement over much greater distances is difficult to assess, but, after nearly a century of analysis, phytogeographers have proposed that postglacial tree distributions in Europe and North America may have advanced at rates of 150 to 500 m per year (Clark *et al.*, 1998). It is certain that northern species migrated southward during cold intervals to mingle with southern species and create a “mixed” flora that no longer exists today. The speed with which the plants moved southward has not been evaluated, but northward plant migration has been studied by a number of researchers (Pitelka & the Plant Migration Working Group, 1997; Clark *et al.*, 1998). The latter authors describe “Reid’s Paradox,” which examines how plants followed the deglaciation of the British Isles and the European continent. They propose that sometime between the end of the last ice age and the Roman occupation of Great Britain, temperate taxa, including oak, migrated 1,000 km to the north. Pitelka & the Plant Migration Working Group (1997) estimate that, for the latest period of glacial withdrawal in eastern North America rates of northward plant migration might have been as rapid as one kilometer per year in the case of *Fagus grandifolia*. During the LGM temperate species of oaks were confined to the region south of latitude 34°N, where they comprised approximately 20% of forest vegetation. By the early Holocene they were present in the Great Lakes region, and mixed mesophytic forests had expanded tenfold (Delcourt, 2002). Thus, the postglacial flora of the Southeast included colonizing species that had arrived since the LGM, and community composition had changed in response to changing climates. McLachlan & Clark (2004) review some of the uncertainties in estimating migration speed (see also Section VIII).

Remarkable continuity and yet very high rates of change characterize the vegetational history of Pleistocene North America. From the perspective of continuity, plant species tend to retain their environmental preferences over long periods (T. Webb *et al.*, 2003). Further, most of the few plant species that vanished from the record during the Pleistocene did so approximately 1.7 ma ago, at the beginning of the Epoch (Jackson & Weng, 1999). Conversely, most plants tend to disperse rapidly, forming a kaleidoscope of fleeting associations with other plants (variously termed “disharmonious,” “non-analog,” and “intermingled”) as their component species track species-specific optimal environments (Graham, 1986). Warm interglacial intervals occur for only approximately 10–30 ka of a 100 ka glacial cycle (North Greenland Ice Core Project Members, 2005; Heusser & Oppo, 2003; Raymo *et al.*, 2004; Raynaud *et al.*, 2005), so that cold glacial-age floral associations presumably endured much longer than their mixed interglacial counterparts. Plant dispersal rates would have

varied according to ability to colonize substrata, ranging from glacial tills to ancient forest soils (Webb *et al.*, 2003; Jackson & Williams, 2004; Williams *et al.*, 2004). Some species were able to survive in small “refugia” in which environments once widespread still persisted, and from which they dispersed upon the return of favourable conditions (James, 1961; Delcourt, 2002; Zazula *et al.*, 2007). By these means most plant species were able to accommodate climatic change in North America throughout the Pleistocene.

Plant associations defined not by species content, but by plant functional types, temperature and rainfall (“biomes”: Whittaker, 1975; Webb *et al.*, 2003; Williams *et al.*, 2004) were usually disrupted within a few thousand years during intervals of rapid post-glacial change. Species typically passed quickly through a given biome en route to more favourable situations. Biomes tended to expand and contract with changing climates, or even disappear altogether. Thus, several modern biomes (e.g. Temperate Deciduous Forest) were rare in North America at the LGM, whereas others (e.g. Mixed Parkland) that were once widespread have virtually disappeared (Webb *et al.*, 2003; Williams *et al.*, 2004). Rates of vegetational (biome) change were greatest between 13,000 and 11,000 cal y BP, coinciding with the rapid retreat of the mid-continental ice sheet (Williams *et al.*, 2004). Some biomes present in the previous (Sangamonian) interglacial, such as Warm Mixed Forest Biome (Heusser & Oppo, 2003) and Taiga Biome (Muhs, Ager, & Begét, 2001), expanded anew during the current interglacial (Williams *et al.*, 2004). It is well known that fire and megaherbivore browsing also tend to promote the extent of grasslands at the expense of forests (Whyte, van Aarde, & Pimm, 2003; Bond, 2005). Open habitats may have been more extensive in the Southeast than closed forests during the late Pleistocene, whereas closed forests are typical of extant, undisturbed forests. The extinction of herbivores and removal of their browsing effects during the Holocene has been seen as contributing to floral change (Webb *et al.*, 2004; Webb & Simons, 2006).

(2) Late Pleistocene flora of the Southeast

James (1961) proposed a hypothetical “Orange Island Refugium” in Florida that sheltered plant and animal species through the many climatic and sea level changes of the late Cenozoic. Although unable to document the existence of a large island refuge, he concluded that the survival of endemic/disjunct terrestrial biota in Florida was likely to be due to the presence of several small islands over the Ocala Uplift that served as an “asylum,” or refuge for Neogene and Quaternary floras. He recognized the possibility that small islands would promote endemism and provide dispersal routes for post-Pleistocene species that had survived regional inundations. Abundant palynological evidence implies that climates south of the continental glacial front were more equable than at present, with warmer winters and cooler summers (Watts & Hansen, 1988; Jackson *et al.*, 2000). At the beginning of the Sangamonian interglacial (~130 ka BP) pollen blown

300 km from the coast of Georgia and South Carolina records an abrupt transition from cool conditions (abundant pollen of *Pinus* and *Picea* species) to warm and dry climates (*Quercus* spp. and herb-dominated pollen) (Heusser & Oppo, 2003). Megafloreal data also document the presence of species of pine, formerly believed to have been restricted to Florida during the Wisconsinan, as far north as Savannah, Georgia (Booth, Rich, & Jackson, 2003), suggesting the presence of very mild weather at that latitude in spite of the presence of continental glaciers in New England.

Biome reconstructions (Webb *et al.*, 2003; Williams *et al.*, 2004) suggest that Floridian vegetation at the LGM generally resembled that of the present. However, deciduous trees and shrubs were less common, and pines, grasses and sedges were more widespread, implying more open landscapes. The southern tip of Florida was occupied by a steppe biome, which briefly expanded into central Florida twice, 18,000 cal y BP and again 9,000 cal y BP. Xeric prairies and salt flats were present about 17,500 cal y BP ago in the vicinity of a rich megafaunal site in the north-western part of the state (Hansen, 2006). Climates became wetter in Florida around 13,000 cal y BP, as the Warm Mixed Forest Biome expanded from northern Florida into southern Atlantic lowlands. Southern pines replaced oaks after 8,000 cal y BP, and plants more typical of the mid-Pleistocene dry interval became restricted to central Florida (Hulbert, 2001). The Warm Mixed Forest Biome dominates south-eastern lowlands today, with the Temperate Deciduous Forest Biome occupying Southern Appalachian highlands (Webb *et al.*, 2003; Williams *et al.*, 2004).

The width of peninsular Florida more than doubled with the drop in sea level during the LGM. A reconstruction (Donoghue, 2006) as it appeared before post-LGM rises in sea level shows broadly exposed lowlands in the region that included all of Florida Bay south of the Florida Keys, and a broad coastal plain west of Tampa. *Nymphaea* sp. peats accumulated early in the sedimentary sequence of Florida Bay (Spackman *et al.*, 1976), and broad expanses of saline marshland formed near Tampa Bay (Rich, 2004). Elsewhere lower water tables promoted the formation of sinkholes and caves in which the remains of Pleistocene plants and vertebrates are preserved (Watts & Hansen, 1988; Webb, 2006). Grimm *et al.* (1993) studied one of the longest terrestrial records of plant communities yet discovered in the Southeast at Lake Tulane, Florida. In it is preserved a nearly 50,000 year pollen record of oscillations between floras characterized either by *Pinus* or *Quercus/Ambrosia* species. *Pinus* spp. fluctuations between approximately 10 and 60% were interpreted to represent major changes from pine forest to open oak-savanna or grassland. The extent of Floridian prairies waxed and waned with changing climates, although they represented a significant part of the landscape for much of the last 50,000 years.

A study conducted at Chatterton Springs, Georgia, indicates that a warm-temperate wetland flora remained intact at that location for thousands of years, with no significant changes in species composition, in spite of the fact that communities surrounding the site underwent dramatic alterations (Seielstad, 1994). The discovery of boreal plant pollen in deposits in coastal South Carolina

posed problems for the “fixed” view of plant communities that prevailed during the mid-Twentieth Century. Frey (1952) recorded high percentages of spruce pollen in salt marsh peat that had accumulated near Myrtle Beach, South Carolina, which he interpreted to be of Wisconsinan age (see below). Such discoveries compelled later workers to re-evaluate the nature and origin of the South-eastern flora. In his analysis of Pleistocene pollen- and spore-bearing deposits from the Southeast, Whitehead (1963) identified a number of “northern” plants, including *Lycopodium lucidulum*, *L. annotinum*, *Sanguisorba canadensis*, *Schizaea pusilla* and *Arceuthobium pusillum* (a woody half-parasite that lives chiefly on black spruce; Gleason & Cronquist, 1963). He later (Whitehead, 1965) concluded that the composition of Pleistocene plant communities must be re-evaluated, observing that, with reference to the Myrtle Beach peat deposit studied by Frey (1952), the association of pollen of a number of relatively thermophilous trees (plants of the southern evergreen forest) with that of spruce made it difficult for him to visualize the deposit as representing a typical boreal forest. He further suggested that full-glacial forests consisted of a mixture of boreal and austral species, a contention that we continue to make here.

It is now recognized that the transient co-occurrence of “warm-” and “cool-climate” taxa was common in the Southeast during the late Pleistocene. Additional examples include a coastal/maritime forest that occupied the vicinity of Gray’s Reef National Marine Sanctuary, located approximately 28 km east of the Georgia mainland in an area currently submerged beneath about 18 m of sea water. The palynological composition of three sediment samples from the Reef is shown in Table 2. Samples of medium grey clay with shell fragments were recovered 5–10 cm below the top of two sediment cores. Pollen/spore recovery was excellent, and included such common taxa as *Pinus*, *Quercus*, *Carya* and *Liquidambar*. Other taxa, however, including *Alnus*, *Picea* and *Tsuga*, typically occur today in more northerly latitudes (Rich & Pirkle, 1994). Watts, Hansen & Grimm (1992) illustrate two horizons in a sediment core from Camel Lake, Florida, in which *Picea*, *Carya*, and *Fagus* species pollen co-occur. The “*Carya/Picea* peak,” as they termed it, was probably derived from a community similar to those now existing in the Great Smoky Mountains and in southern Quebec. An association of *Liquidambar*, *Pinus*, *Quercus*, *Taxodium* and *Gordonia* species was discovered in a pre-LGM (>47,470 ¹⁴C y BP) beaver pond deposit near Deepstep, Georgia (Rich *et al.*, 2000). With the exception of *Gordonia* sp., this assemblage mirrors the pollen assemblage of the Gray’s Reef samples. Species records abundantly document the presence of “mixed” late Pleistocene-early Holocene floras in Florida and the southern Atlantic seaboard.

(3) Southeastern prairie - a vanished habitat

Evidence of ancient prairie floras in the Southeast has increased steadily over the last three decades. The term “Prairie” usually refers to the xeric communities of the Midwest and Great Plains, whereas in the Southeast it is also applied to *Nymphaea* wetlands, such as Chesser Prairie,

in the Okefenokee Swamp, and Paines Prairie, near Gainesville, Florida. Whitehead (1965) flatly declared that prairies lie west of deciduous forests and occupy vast regions of interior North America, as though there were no possibility of their having once occupied the eastern seaboard. The possibility that prairie vegetation, like boreal forest or south-eastern evergreen forest, could blend into other plant communities simply was not considered when, for example, Braun (1950) mapped the distributions of North American forests. It is generally recognized now, however, that prairies in the sense of the grass-dominated communities of the Great Plains were once a significant element of the Southeastern flora.

Current palynological data show that grasses (Gramineae/Poaceae) were present during the Oligocene (Traverse, 1988). While their early history is poorly understood, it is clear that grasslands covered areas of the Atlantic Coast during the late Tertiary and very early Quaternary. Groot (1991) surveyed pollen samples from a number of localities on the Atlantic coastal plains of New Jersey, Delaware, Maryland, and Virginia. In his Cape May County Airport (New Jersey) borehole, samples from a depth of 29.57–47.26 m contained 40–58% oak pollen. Pollen from other tree genera included that of *Pinus* (2–11%), *Liquidambar* (1–10%), *Carya* (1–20%), *Betula* (2–7%) and *Alnus* (1–5%). Tree pollen was accompanied by that of herbaceous taxa, including rare *Artemisia*, and low levels of pollen of Caryophyllaceae/Chenopodiaceae, Compositae and Gramineae. Caryophylls and chenopods were most abundant among the herbaceous plant pollen types, ranging from 2–13%, with composites ranging from 1–7%, and grasses between 1 and 4%. The deposit is probably of Quaternary age, for it lacks extinct or extirpated species that occur at greater depths. Wetland plant taxa and algal remains were either absent, or present in only trace amounts. Although more strata on the East Coast of this age should be sampled, it appears that the vegetation preserved in the Cape May County locality was derived from a pine-oak-hickory savanna.

Mid-Twentieth Century pollen studies hinted at the possibility that expansive herbaceous communities, not necessarily associated with tundra, might have occupied the Southeast during the later Pleistocene. In his analysis of strata from Singletary Lake, a Carolina bay in eastern North Carolina, Frey (1951) noted that, below a pine-spruce pollen zone dated at >20,000 ¹⁴C y BP there were abundant grasses, composites, and sedges which are normally associated with open-ground vegetation with only scattered trees. Frey (1952) described the pollen composition of samples taken from the Horry Clay, near Myrtle Beach, South Carolina. He observed that pollen of grasses and composites was quite abundant in some samples (44.5:3.2%, 34.5:14.9%, and 55.8:24.2% in three of his samples, respectively). There was also pollen of shrubs, and pteridophyte spores in some of the samples. His interpretation of these data was that land areas surrounding the site of deposition were only sparsely wooded, and were more typically covered with various herbs, shrubs, and ferns growing under fairly moist environmental conditions.

Frey (1953) combined data from eight sites in eastern North Carolina to present a generalized pollen diagram

illustrating changes in abundances of twenty taxa/groups of pollen and spores dating back to a putative Peorian (Early Wisconsinan) age. It is known that strata in his pollen zones N, O, and P are older than 20,000 ¹⁴C y BP (N is highest in the section and, therefore youngest, with O and P being successively older). From the upper limit of zone N down through P, prominent taxa include *Quercus*, *Carya*, *Fagus*, additional broadleaved trees and shrubs, grasses, composites, and sedges, with a commensurate decrease in pine. Frey (1953) observed that the composition of the palynoflora usually would be interpreted to indicate treeless conditions at the time of deposition; he preferred an interpretation showing that the sample sites themselves (Carolina bays) were treeless and that non-arboreal vegetation surrounding the basins simply out-produced the trees that did grow outside the bays. In any case, the likelihood remains that currently forested Carolina bays then resembled marshes or prairies.

As more sites came under investigation in the South-east in the 1970s and 1980s, the former extent of grasslands became more apparent. Watts (1971) obtained samples from Lake Louise, Georgia, and, in reference to his pollen zone M2 (dating from approximately 5,000 to 8,100 ¹⁴C y BP), observed that apparently sclerophyllous or scrubby oak-hickory vegetation was present, and it was accompanied by herbaceous plants such as those that characterize the prairie in the upper Midwest. He further noted that the herb assemblage, which included the Gramineae, Cyperaceae, *Ambrosia*, *Artemisia*, *Iva*, other composites of the Tubuliflorae, *Chenopodium*/*Amaranthus*-type, and *Lechea* was remarkably like that characterizing prairie in Minnesota, an area with which he was quite familiar. Watts (1971) argued that small prairies and oak savanna near Lake Louise and Mud Lake, Florida, approximately 8,500–5,000 ¹⁴C y BP could have supported grazing and browsing animals. After forest canopies closed about 5,000 ¹⁴C y BP the habitat would have become markedly less suitable for large herbivores.

Rich (1979, 1984) collated an extensive set of palynological data from the Okefenokee Swamp, in south-eastern Georgia, including analyses of basal samples from several sites in the eastern half of the swamp basin. The samples all predated the onset of substantial peat development, and are therefore believed to represent the character of the vegetation of the primordial Okefenokee Basin. Based on the presence of pollen of herbaceous species, and the absence of pollen of typical evergreen forest plants, he concluded that, between 6,600 and approximately 2,000 ¹⁴C y BP, marshes mixed with wet-mesic and mesic prairies extended over the basin, with sand hills covered by xerophytic grasses (*Andropogon* spp.) as well as composites and chenopods which frequently accompany modern prairies; such communities are still common on the sand ridges that border many streams in the Southeast. Late Pleistocene prairie floras were also described by Watts *et al.* (1992) from Camel Lake, referred to above. Between 14,330 ± 275 and 12,610 ± 135 ¹⁴C y BP, and coincident with one of the *Carya*/*Picea* abundance peaks, were minor but significant peaks in abundances among prairie plants (*Ambrosia*, *Artemisia*, *Iva*, Gramineae). The authors acknowledge that the mixture of broad-leaved-forest and prairie plants was “curious,” alluding, it seems, to the

unlikely association of hickory/spruce vegetation with prairie herbs. Certainly, for samples from the Southeast this would still strike one as curious except that we now know much more about the palaeoecology of this region.

The palynological, sedimentological, and dendrological composition of a buried forest site in Coffee County, Georgia, led Zayac, Rich & Newsom (2001) to conclude that the depositional environment resembled the modern Platte and Saskatchewan River basins. The trees, two of which were dated at $6,870 \pm 50$ and $5,050 \pm 50$ ^{14}C y BP, apparently grew either in a prairie or southern pine savanna community with abundant grasses. Thus, the climate, composition and distribution of the flora, and geography of the area differed greatly from present conditions. The faunas we depict in this study evolved in a dynamic balance with that ancient landscape. Finally, during early historical times, Spanish explorers in the Carolinas described prairie vegetation up to 40 km across, created through repeated Native American burning. These tall-grass stands have since been replaced by broadleaf forest, and subsequently by farms and cities, and have virtually passed from memory (Barden, 1997; Anonymous, 2002). A small parcel of Carolina prairie is now in the process of being reconstructed at the North Carolina Museum of Natural Sciences (M. A. Brittain, personal communication, 2007).

V. THE PALAEOZOOLOGICAL ENVIRONMENT

(1) Pleistocene mammalian associations in North America

In North America during the Pleistocene, patterns of change in mammalian species in space and time were similar to, but not identical with those of plants. Such patterns have been carefully studied in the postglacial flora and fauna of Europe (Hewitt, 2000). The diversity of large mammals (>45 kg adult mass) in North America north of Mexico slowly increased through the Pleistocene (from 1.7 ma), largely due to immigration from South America and Asia across (respectively) the Panamanian and Beringian isthmuses (Bell *et al.*, 2004; Martin, 2005). The generic-level extinction rate for large mammals during the Pleistocene was approximately 5 per million years. They were thus comparable to, or lower than mammalian extinction rates during the Cenozoic (Alroy, 1996, data in Martin, 2005). This consistency is remarkable, considering that during the Pleistocene the continent experienced frequent and massive alternations of glacial and interglacial climates (Raymo, *et al.* 2004; McNeil *et al.*, 2005). The terminal Pleistocene North American Rancholabrean Land Mammal Age (defined by the appearance of the genus *Bison* in mid-latitudes; note that older records of *Bison* may occur in Florida: Webb *et al.*, 2004) began before the conclusion of the penultimate (Illinoian) glaciation. The Rancholabrean continued through the Sangamonian Interglacial and Wisconsinian Glaciation, to end with the megafaunal extinction well into the interval of post-glacial melt. Counterintuitive although it may seem, no temporal

subdivisions of the Rancholabrean Age have yet been resolved based on changes in the species composition of the North American mammalian fauna (Bell *et al.*, 2004).

Two-thirds of large mammals then in North America north of Mexico vanished in the late Pleistocene extinction interval (Bell *et al.*, 2004; Martin, 2005; Morgan, 2005). At high latitudes, the contrast between pre-extinction abundances of the genera *Spermophilus*, *Equus* and *Mammuthus*, and the post-extinction abundance of *Marmota*, *Alces* and *Rangifer* (Harrington, 2003) illustrates the great amplitude of the faunal change. Plants heavily dependent on megafaunal species for dispersal (e.g. *Gleditsia triacanthos*, *Gymnocladus dioica*, *Machura pomifera* and *Proboscidea* spp.) underwent severe restrictions in range (Barlow, 2000). In Florida, the largest surviving megafaunal species is *Odocoileus virginianus* (mass 100 kg: Webb & Simons, 2006). In New York, a crash in the abundance of spores of dung fungi approximately 12,200 ^{14}C y BP closely followed an increase in charcoal deposits of possible anthropogenic origin. The latest megafaunal skeletal occurrences in New York date from approximately 11,000 ^{14}C y BP, and precede the final glacial advance (Younger Dryas) of the Pleistocene (Robinson, Burney & Burney, 2005). In Florida, the oldest widely accepted evidence of Palaeoindian activity dates from about 12,400 ^{14}C y BP (Dunbar, 2006), and the megafaunal extinctions are estimated to have taken place between 12,400 and 10,000 ^{14}C y BP (approximately 15,000 and 11,500 cal y BP), and probably closer to the latter date (Webb & Simons, 2006). It is possible that the extinctions, at sites about 1,600 km apart (New York and Florida), occurred at approximately the same time, following more than a millenium of human-megafaunal coexistence (Robinson *et al.*, 2005; Webb & Simons, 2006). Mammoth trackways in southern Alberta also dating from approximately 11,000 ^{14}C y BP show an age distribution suggestive of a declining population (McNeil *et al.*, 2005). The youngest occurrence of mammoths in North America is currently suggested to be approximately 4,500 to 3,500 ^{14}C y BP on St. Paul Island in the Bering Straits off Alaska (Veltre *et al.*, 2008).

As is generally the case in plants, preferred ecological niches for mammals apparently remained unchanged through the late Pleistocene. Niche projections for six of eight mammalian species that became extinct actually expanded into the Holocene. In all probability *Mammut americanum*, *Mammuthus columbi*, *Equus conversidens*, *Platygonus compressus*, *Bison antiquus* and *Oreamnos harringtoni* could flourish today on this continent. Only *Canis dirus* and *Camelops hesternus* would experience range restrictions (by 29.6% and 16.6%, respectively: Martínez-Meyer, Peterson & Hargrove, 2004). It may be significant that, following the collapse of Native American populations resulting from the introduction of European diseases, populations of feral *Equus caballus* and indigenous *Bison bison* rapidly proliferated across mid-latitude North America (Martin, 2005). Game reserves with large populations of native species were established in Africa in regions where disease vectors prevented the establishment of resident populations of humans and their domestic animals (Bengis, Grant & de Vos, 2003). Similarly, following the expulsion of humans from the vicinity of the Chernobyl nuclear disaster, the region has become a rich

wildlife refuge containing flourishing populations of large mammals and possessing the potential of becoming the largest game reserve in Europe (Mycio, 2005).

Although *Mammuthus* spp. groups typically remained within a relatively restricted area, *Mammuthus americanum* possibly traversed as much as 500 km in the course of seasonal migrations (Koch, Hoppe & Webb, 1998; Hoppe *et al.*, 1999). Mobility and population pressures over time scales of centuries may have contributed significantly to range extension in some megaherbivore species. It is noteworthy that during the LGM many extinct megafaunal taxa were distributed from the subtropics to the arctic, and from the Atlantic to the Pacific Coast (e.g. *Arctodus simus*, *Bison* spp., *Equus* spp., *Dinobastis serus*, *Mammuthus americanum*, *Mammuthus columbi*, *Megalonyx* sp., *Panthera leo atrox*, *Platygonus compressus*; see Hullbert, 2001; Stock & Harris, 2001; Harington, 2003). They probably did not frequent ice fields, so that absence of fodder rather than cold may have limited their distributions. Yet, in response to global warming, mammal distributions have generally expanded even from small glacial-age refugia, as has been confirmed by genetic evidence (Lessa, Cook & Patton, 2003; Rowe *et al.*, 2004).

Isotopic, taphonomic and dental evidence suggest that individual megafaunal species tended to frequent certain environments. The scimitar cats (*Dinobastis serus*, *Smilodon fatalis*) hunted in woodland-grassland mosaics where a diversity of prey could be located and easily ambushed (Marean & Ehrhardt 1995; Kohn, McKay & Knight, 2005). *Bison* spp. and *Mammuthus columbi* were dedicated grazers, preferring prairie environments (Koch *et al.* 1998; Hoppe, Paytan & Chamberlain, 2006); it should be noted that during the late Pleistocene *Bison* spp. diets included a greater variety of browse than they do at present (Rivals, Solounias & Mithlacher, 2007). *Equus* spp. also sought out grasslands, but often supplemented diets by browsing on shrubs and trees (Hoppe, Stuska & Amundson, 2005). *Hemiauchenia macrocephala* preferred open woodlands (Kohn *et al.*, 2005). *Mammuthus americanum* was a browser in the manner of rhinos and moose, engaging in bark stripping and munching foliage, twigs and fruit (Green, Semprebon & Solounias 2005; Newsom & Mithlacher, 2006). Xenarthrans were browsers as well, preferring low, coarse vegetation (*Holmesina septentrionalis*), leaves, twigs and nuts (*Megalonyx jeffersoni*), wet, riparian herbs (*Glyptotherium floridanum*), intermediate level browse (*Paramylodon harlani*) and higher level browse (*Eremotherium laurillardii*) (McDonald, 2005). Closed-canopy forests were the preferred habitat of *Mylohyus fossilis*, *Tapirus veronensis*, *Odocoileus virginianus* and *Palaeolama mirifica* (Koch *et al.*, 1998; Kohn *et al.*, 2005).

As in the case of plants, it has been widely postulated that mammalian associations are transient, and that mammals change their ranges according to individual species preferences (Graham, 1986; FAUNMAP 1996; Stafford *et al.*, 1999). Yet, in a study based on associations enduring 1 ma, and separated by as much as 3,500 km, McGill, Hadley & Maurer (2005) found quantifiable evidence that during the Pleistocene small mammals, for unspecified reasons and in spite of major environmental changes, tended to associate in communities. Various authors have regarded late Pleistocene-early Holocene floral associations in eastern North America as

biomes (e.g. Williams *et al.*, 2000), and cold Arctic grasslands that were extensive during the LGM have been termed a “Mammoth Steppe Biome” (Zazula *et al.*, 2007). Perhaps FAUNMAP (1996) “faunal clusters” could in some respects be regarded as analogous to floral biomes.

(2) Wisconsinan (Late Pleistocene) vertebrates of the Southeast

(a) Florida

Of the 81 amphibian and reptilian species present in the late Pleistocene of Florida (Table 3), 95% are still present in the state (four extinct species or subspecies, and one extirpated species that occurs in contiguous states are lacking). The distributions of most of their modern counterparts extend along the Atlantic Coastal Plain towards the north-east (Ashton & Ashton 1988). In striking contrast, of the 92 mammalian species inhabiting Florida during the Late Pleistocene, approximately 50% have since become either extinct (35 species) or extirpated (11 species; see also Webb & Simons, 2006). Due to changing climates and species-specific preferences, biota inhabiting the Southeast during the late Pleistocene appeared to be “mixed” relative to modern biota, which have since regrouped into observed modern associations. Formerly common large mammalian herbivores included proboscideans, xenarthrans, *Bison* spp. and *Equus* spp., which were preyed upon by large felids, machairodonts and *Canis dirus*. The number of *Mammuthus columbi* localities (18) is approximately equal to that of *Mammuthus americanum* (20; see Table 2.1 in Webb, 1974). Other “exotic” components of Floridian assemblages were *Hesperotestudo crassiscutata*, giant birds (ciconiids and vulturids), large cingulates and a large species of *Desmodus*. In Florida, as in non-glaciated regions generally, the tempo of postglacial climatic change is often suggested as a contributing factor in megafaunal extinctions (Roth & Laerm, 1980; Bentley, Knight & Knoll, 1994; Bentley & Knight, 1998; Hullbert, 2001; Holman, 2000, 2001, 2003; Webb & Simons, 2006).

For modern species distributions and environmental preferences of Floridian amphibians and reptiles, see Ashton & Ashton (1988) and Palmer & Braswell (1995); for distributions of extant mammals, see Burt & Grossenheider (1980) and Nowak (1999). Among the animals occurring in the late Pleistocene of Florida, the following species were probably adapted to prairie environments, and occur in the fossil record of Florida and elsewhere in the southern Atlantic region. They include: *Gopherus polyphemus*, *Terrapene carolina putnami*, *Hesperotestudo incise*, *Hesperotestudo crassiscutata* (giant tortoise), *Cnemidophorus sexlineatus*, *Sceloporus undulatus*, *Heterodon platyrhinos*, *H. simus*, *Drymarchon corais* (associated with turtle burrows), *Reithrodontomys humulis*, *R. fulvescens*, *Podomys floridanus* (associated with turtle burrows), *Sigmodon hispidus*, *Geomys pinetis*, *Conepatus leuconotus*, *Canis* spp., *Miracinonyx trumani*, *Mammuthus columbi*, *Equus* spp. and *Bison* spp.

(b) Virginia

Most (approximately 80%) of the mammal-bearing sites in Virginia occur in the Appalachian region, where about

half are preserved in cave, karst or fissure-fill deposits (McDonald *et al.*, 1998). The record of small vertebrates is accordingly relatively well sampled (Table 3). All Wisconsin genera known within the state have been recorded in the Appalachian region. *Homo sapiens*, *Sciurus carolinensis*, *Castoroides ohioensis*, *Canis diris*, *C. latrans*, *C. lupus*, *Ursus americanus*, *Mammuthus americanus*, *Mammuthus primigenius*, *Equus* spp., *Mylohyus fossilis*, *Rangifer tarandus*, *Bootherium bombifrons* and *Bison* spp. are also recorded in lowland deposits near or within the coastal plain.

The ratio of the number of lowland sites (excluding one that yielded only a walrus record) to the total number of sites throughout the state is 14/93 or 15%. The ratio of the number of sites recorded per genus in the coastal plain to the number of sites per genus throughout Virginia is 1.73/6.73 or 26%. A comparison of these two ratios suggests greater faunal homogeneity in lowlands. This may be due to the environmental uniformity of lowlands relative to mountainous terrain, or to the relatively larger size of mammalian genera so far recovered from the Virginia lowlands, or both. Mountainous regions are generally not well sampled in the Appalachian region to the south.

Reviewing mammal-bearing sites throughout Virginia, McDonald *et al.*, (1998) observed that the most commonly occurring large herbivores were *Odocoileus virginianus*, *Mylohyus fossilis*, *Equus* spp. and *Mammuthus americanus*. Unlike the situation in Florida, where *Mammuthus americanus* and *Mammuthus* spp. sites are approximately equal in abundance, the former are three times as common as *Mammuthus primigenius* sites in Virginia (a ratio of 4:12). The dominant large carnivores were *Canis diris* and *Ursus americanus*, although *Panthera leo atrox* was also present. In Florida, mylodonts and llamas were common, and large felids were among the dominant carnivores. A comparison between relative diversities of vertebrate subgroups listed in Table 3 suggests that insectivores, rodents and artiodactyls were relatively more diverse in Virginia, and turtles, lizards and edentates relatively more diverse in Florida. Overall species similarity is 48% between Virginia and Florida. The presence of a north-south faunal gradient is thereby inferred.

From their present (Banfield, 1974) and/or Pleistocene distributions, the following taxa strongly suggest that late Pleistocene climates in Virginia were cooler than at present: *Sorex arcticus*, *Ochotona* spp. indet., *Lepus americanus*, *Eutamias minimus*, *Phenacomys intermedius*, *Microtus xanthognathus*, *Synaptomys borealis*, *Martes americana*, *M. pennanti*, *Mustela erminea*, *Mammuthus primigenius*, *Alces alces*, and *Rangifer tarandus*.

Fewer possibly "prairie" species are present than is the case for Florida: *Heterodon platyrhinos*, *Lampropeltis calligaster*, *Cryptotis parva*, *Spermophilus (Citellus) tridecemlineatus*, *Mammuthus primigenius*, *Equus* spp. and *Bison* spp.

McDonald *et al.*, (1998) cite changes in the distributions of plants and animals at the end of the Pleistocene in Virginia as evidence of major climatic warming accompanied by a wetter environment with less pronounced extremes of temperature and precipitation than had existed under the glacial climatic regime. Periglacial/boreal conditions with relict populations persisted only at higher elevations in western Virginia. However, in Florida the most

prominent climatic change at the end of the Pleistocene was an increase in humidity (Webb *et al.*, 2003; Williams *et al.*, 2004, see Section IV.2).

The pattern of vertebrate extinctions in the two regions also differs. For amphibians and reptiles, the proportion of extinctions and extirpations is relatively small in both regions (~5%). This proportion for mammals in Virginia, approximately 35%, is less than the value of 50% for Florida. The ratio of extirpated to extinct species was greater in Virginia than in Florida (12/19 or approximately 60% versus 11/35 or approximately 30%). In Virginia, extirpated mammalian species tended to move into recently deglaciated regions toward the north-west. In contrast to the mammalian response, all of the listed amphibians and reptiles remain in Virginia today, with the exception of an anuran and chelonian that occur in the nearby western watershed of the Appalachians (Harding 1997).

(c) Georgia

The vertebrate record in Georgia may be separated into two distinct regions. One, from the interior of the state, is dominated by small vertebrate remains recovered from cave deposits (Table 3, north-west Georgia localities) and has similarities with both the Virginia and the Florida assemblages (Martin, 2001). The other, from the coastal region (Table 3, coastal Georgia localities), appears to be identical to that of Florida.

The Pleistocene megafauna of coastal Georgia is historically important (Lipps, Purdy & Martin, 1988). During the first half of the 19th Century, it yielded the type specimen of *Mammuthus columbi* (now in the Natural History Museum, London, UK), and a nearly complete skeleton of *Mammuthus americanus* reputed (incorrectly) to be in the collections of the Museum national d'Histoire naturelle, Paris (P. Tassy, personal communication 2004). However, megafaunal diversity in this region has been only incompletely documented. A major site is apparently of Sangamonian (last interglacial; Hulbert & Pratt, 1998) age, predating the LGM and Wisconsinan period. Mild climates in coastal Georgia are indicated by the presence of *Alligator mississippiensis* and large terrestrial turtles. The latter, in addition to the *Signodon hispidus*, *Mammuthus columbi*, *Equus* sp. and *Bison* spp. are suggestive of extensive grassland environments. The presence of *Leopardus* sp., *Palaeolama mirifica* and diverse edentates implies that more complete sampling would reveal a diverse Floridian megafauna (Mead & Spell, 2003).

(d) South Carolina

Bone and tooth fragments strongly support the presence of virtually the entire Floridian megafauna in South Carolina during the Wisconsinan, with the exception (thus far) of large vampire bats (*Desmodus* sp.) and cheetahs (Roth & Laerm, 1980; Bentley *et al.*, 1994; Sanders, 2002). However, a cheetah (*Miracinonyx trumani*) has been recorded in older strata within the state (late Irvingtonian; McKay, Kohn & Knight, 2004). Tooth occurrences of *Mammuthus columbi* and *Mammuthus americanus* are about equally abundant (11:14;

Roth & Laerm, 1980; Bentley *et al.*, 1994; Sanders, 2002). Remains of large terrestrial tortoises (*Terrapene carolina putnami*) and *Alligator mississippiensis* imply the presence of subtropical, frost-free climates and warm, moist savanna habitats in lowland South Carolina at a time when late Wisconsinan ice covered the northern continental interior (Roth & Laerm, 1980; Sanders, 2002). Presently submerged margins of the coastal plain were well vegetated and supported populations of the large bison (*B. antiquus*) and a diverse vertebrate fauna. Environmental requirements of turtles suggest the presence of savanna grasslands interspersed with freshwater streams and hammocks of shrubs and trees, in turn frequented by browsing herbivores (Sanders, 2002). No cold-adapted taxa, such as appear in Virginia and to a lesser extent in the interior of Georgia, are recorded from coastal South Carolina. However, a few species that also occur in Virginia suggest cooler facies assemblages may have been present in areas at some distance from the coast. These include: *Spermophilus (Citellus) tridecemlineatus*, *Synaptomys cooperi*, *Equus complicatus*, *Cervus elaphus*, and *Mylohyus nasutus*.

(e) *North Carolina*

Many species not documented in the fossil record of North Carolina have been recorded in the Wisconsinan of Florida through South Carolina and to the north into Virginia. Because they occur to the north and south of North Carolina, continuity of habitat suggests that they were also present in the Wisconsinan of this state as well. Broad distributions imply significant faunal uniformity along coastal lowlands throughout the region, as well as the presence of a vertebrate assemblage resembling that of Florida. However, many species recorded in Virginia also occur within the interior of Georgia to the south-west, and probably inhabited mountainous regions of North Carolina (Grady, Hubbard & Holler, 1998). The distribution of these species defines an “interior” faunal facies that did not resemble the Floridian assemblage as closely as did the coastal faunal facies. It was associated with the Appalachian region, which approaches the Atlantic coast in Virginia. As noted before, the Appalachians remained free of glacial ice throughout Pleistocene time.

West Virginia occurrences of two Floridian taxa (*Desmodus* sp. and *Smilodon fatalis*) predate the LGM, and possibly reflect interglacial climatic conditions (Grady & Garton, 2000; Grady, Arroyo-Cabrales & Garton, 2002). Vertebrate fossils have been found across the North Carolina coastal plain to the east, but in most cases their age is poorly constrained (Table 3). The faunal and environmental information they convey pertains to the late Pleistocene in general, rather than only the Wisconsinan. Because glacial intervals were longer than interglacials during the Pleistocene, and because glacial-age environments along the southern Atlantic coast are postulated to have been mild (see below), these occurrences are provisionally taken as generally representative of the Wisconsinan.

The presence of *Alligator mississippiensis*, the large box turtle *Terrapene carolina putnami* and the giant *Hesperotestudo crassiscutata* in Pleistocene deposits of North Carolina implies the

existence of mesic climates at least as warm as at present. Floridian elements in the assemblage include *Holmesina septentrionalis*, *Eremotherium laurillardi*, *Hydrochoerus holmesi* and *Mammuthus columbi*. *Mammuthus* spp. occurrences are about half as common as those of *Mammuth americanum* (6:13, records in collections of the NCMNS). The large terrestrial turtles and *Mammuthus columbi*, together with abundant *Equus* spp. and *Bison* spp. occurrences suggest the presence of grassland environments. Conversely, the relative abundance of *Mammuth americanum* and *Odocoileus virginianus*, and records of *Mammuthus primigenius* and *Bootherium bombifrons* lend a transitionally boreal cast to the North Carolina assemblage.

VI. BIOTIC GRADIENTS WITHIN A SOUTH-EASTERN THERMAL ENCLAVE

The regional biological unity of vertebrate faunas inhabiting Wisconsinan-age lowlands bordering the South Atlantic Bight between Cape Canaveral and Cape Hatteras appears to be supported amply by evidence presented in Table 3. Climates were apparently mild and equable, and there are clear floral and faunal indications of the presence of a mosaic of forest, savanna and prairie habitats (Sanders, 2002; Mead & Spell, 2003). A relatively sharp ecological transition (“ecotone”) probably occurred near the latitude of Cape Hatteras (35°N, see also Delcourt, 2002, for floral evidence). As noted before, it is surprising to us that a Wisconsinan glacial front, locally situated approximately 500 km north of the North Carolina-Virginia border and 300 km north of the Potomac River, was unaccompanied by glaciation at high elevations within the southern Appalachians and impacted so little on nearby coastal biota in the Southeast. The extent of the Wisconsinan ice sheet at its maximum was comparable to, albeit smaller than the ice cap presently covering Antarctica (Drewry, 1983; Dyke *et al.*, 2002; Marshall *et al.*, 2002). The occurrence of large terrestrial turtles and alligators so close to the ice front, even if it was in the process of melting, seems anomalous.

Relationships between physical and biological environments often are neither simple nor straightforward. To cite a few general examples, competition between plants utilizing different photosynthetic pathways is affected by heat and carbon dioxide concentrations, isotopic evidence of which is transmitted to the bodies of herbivores (Jackson & Williams 2004; Koch, Diefenbaugh & Hoppe, 2004). Elephant browse and fire both promote the spread of grasslands (Owen-Smith, 1988; Whyte *et al.* 2003; Bond, 2005). Plant distributions are strongly affected by climate, and by the presence or absence of animals that disperse their propagules (Barlow, 2000). A plexus of plant and animal gradients evidently existed east of the Southern Appalachians.

The distribution of plant biomes in the Southeast, as depicted here for the Wisconsinan, shows a floral gradient towards the north (Williams *et al.*, 2000; Jackson & Williams, 2004). The reconstructions show an “Open Conifer Woodland” biome extending from peninsular Florida to the South Carolina-North Carolina border. There it is

replaced sequentially by “Cool Mixed Forest” and “Cool Conifer Forest” biomes to the North Carolina-Virginia border, and by a “taiga” biome north-east of Virginia (see Fig. 3a in Williams *et al.*, 2000). In Virginia, cool conifer forests coincide with the southern edge of the FAUNMAP (1996) “northeast province,” as noted above. Vertebrate faunas exhibit a similar pattern of change. Faunal resemblance (see Section II, Methods) to Florida was found to be approximately the same in the amphibian, reptile and mammalian taxa compiled for each state, and for the Great Lakes region and southern California. Species diversity of all three vertebrate groups was accordingly summed for each of the states/regions to calculate an overall faunal resemblance to Florida. This was found to have declined in a regular manner toward the Great Lakes, about 2,000 km to the north. A similar but shorter (500 km) warm-to-cool gradient evidently extended from the Atlantic coast to the Appalachian highlands in the west (Table 4). “Islands” of tundra occupied the crests of the Southern Appalachians during the LGM (Delcourt, 2002). As previously noted, an Appalachian subregion was characterized by the presence of several species of mammals more typical of the “north-east province.” Interestingly, the fauna of the California site, situated at the same latitude as Florida but about 3,800 km to the west, resembles Floridian assemblages less than those of the colder Great Lakes region (Table 4).

Suggestions of gradients can be perceived at finer scales of resolution. Various lines of evidence suggest that grasses figured prominently in the diets of *Mammuthus* spp., *Equus* spp. and *Bison* spp., (e.g. Harington & Ashworth 1986; Haynes & Klimowicz, 2003), whereas *Mammuthus americanus*, *Tapirus veroensis*, and *Mylohyus fossilis* browsed within dense, often closed-canopy forests (e.g. Koch *et al.*, 1998; Feranec, 2004). The presence of both dietary groups in an assemblage of megaherbivores supports the existence of both prairies and forests (e.g. Sanders, 2002). Furthermore, *Mammuthus-Mammuth* locality ratios decline towards the north, from approximately 1:1 in Florida and South Carolina, to about 1:2 in North Carolina and approximately 1:3 in Virginia. Throughout most of the Great Lakes region, mastodon localities are

three times as abundant as those of mammoths (154:465) except in Wisconsin where *Mammuthus* spp. localities outnumber those of *Mammuth americanus* (28:20; Holman, 2001). That *Mammuth americanus* occurrences increase towards the north suggests that forest cover increased and prairies dwindled. Conversely, in the semiarid grasslands of the south-western United States the number of *Mammuthus* spp. localities exceeds those of *Mammuth americanum* by an order of magnitude (73: 7) and other grazing megaherbivores including *Bison* spp., *Camelops hesternus* (a western species) and *Equus* spp. are also common (Morgan & Lucas, 2005).

In general terms, following the disappearance of continental ice and the megafaunal extinctions, climates became wetter within the “south-eastern (faunal) province” (Webb *et al.*, 2003; Williams *et al.*, 2004), and clearly warmed in the region of Virginia (McDonald *et al.*, 1998). Open conifer woodlands and prairies were supplanted by warm mixed forests over much of the Southeast as interglacial climates stabilized (see above). Vertebrate reactions to the change from Pleistocene “mixed” floras to modern broadleaved floras were evidently not uniform. Surviving endothermic mammals, irrespective of their size, tended to become extirpated in former areas of distribution, presumably following plant redistributions. Many Virginian mammalian species, for example, colonized recently deglaciated terrains (see Banfield, 1974). Although 17% of the Floridian avifauna became extinct, including some of its largest and most widely distributed members, many avian survivors now inhabit areas to the north or west, often in grassland or northern coniferous habitats (Webb *et al.*, 2004). On the other hand, ectothermic amphibian and reptilian species, which as a group suffered only minor extinctions, did not follow floras to the north nearly to the degree show by mammals (Table 5). With the extinction and redistribution of mammalian species, the distinctiveness of the “south-eastern province” was lost near the beginning of the Holocene (FAUNMAP, 1996).

The spectacular megafauna-dominated biota of the Southeast during the LGM and early postglacial interval rivaled that of modern Africa. A growing literature is focused

Table 4. Comparisons, Wisconsin assemblages. Data are compiled from Table 3 and from Holman (2001) and Stock & Harris (1992). Note that species diversity represents the total number of species indicated for diversity values, and minimum number of species for similarity estimates. Similarity is calculated with reference to Florida values; the percentage of mammalian extinctions in the south-eastern United States is calculated only for the more completely sampled mammalian assemblages clustered at the southern and northern ends of the faunal gradient. Except for turtles, herpetofaunas remain unsampled in South Carolina. For further explanation see text

	Species diversity			
	Mammalian	Amphibian & reptile	Similarity	Mammalian extinction
Florida	91	79	100%	37%
Coastal Georgia	40	27	95%	–
South Carolina	52	–	77%	–
North-west Georgia	61	54	68%	–
Virginia	90	48	49%	21%
Southern Great Lakes	65	19	47%	20%
Northern Great Lakes	57	23	38%	16%
California: Rancho La Brea	55	31	31%	38%

Table 5. Species diversity in modern (existing) faunas: Data are taken from range distributions in Ashton & Ashton (1998), Banfield (1974), Brown (1997), Harding (1997), Kurta (1995), Martof *et al.* (1980) and Mitchell (1994). Amphibian and reptile occurrences in the Yukon Territory of Canada were taken from Territorial web sites

	Florida	Virginia	S. Great Lakes	N. Great Lakes	Yukon
Amphibians and reptiles					
Salamanders	24	37	18	7	0
Frogs	28	24	12	11	4
Turtles	20	18	11	6	0
Lizards	17	9	4	1	0
Snakes	39	30	22	11	0
Total	128	118	67	36	4
Mammalian groups					
Insectivores	5	12	11	8	5
Bats	17	12	10	6	1
Rodents	16	25	24	17	23
Carnivores	12	14	24	17	16
Total	56	69	68	54	52
Total above groups	184	187	135	90	56

on the biotic transition between ice age climatic conditions, environmental changes associated with the arrival of humans, and the late Cenozoic history of plants and animals living in the Southeast today. The robust multidisciplinary approach initiated by Webb (2006), and recent advances in nanotechnology (isotope, molecular and high resolution analyses) provide the means to reveal further the dynamics of late Pleistocene-early Holocene ecosystems. The documented presence of three species of elephants in North Carolina alone conjures a proximate but strange past that was once familiar to human inhabitants of the state. Incomplete as existing samples are, they clearly pose questions concerning how comparable the Southeastern vertebrate fauna was to those in other regions of North America.

VII. INTRACONTINENTAL FAUNAL RELATIONSHIPS

The biogeography of Late Pleistocene mammal assemblages across the continental United States was reviewed in detail by FAUNMAP (1996). Species defining a Late Pleistocene “northeastern province” (*Microtus xanthognathus*, *Microtus borealis*, *Sorex arcticus*, *Tamias striatus*, *Blarina* spp. and *Spermophilus tridecemlineatus*) also occurred in Virginia and indicate that the latter state belonged to that province (Table 3). The province extended west across the Great Lakes region, where it was characterized by open parkland containing some boreal forest species. According to FAUNMAP (1996), Florida was biogeographically distinct and characterized by the co-occurrence of *Didelphis virginiana*, *Procyon lotor*, *Sciurus carolinensis*, *Urocyon cinereoargenteus*, *Platygonyx compressus* and *Tapirus* spp. As shown by Table 3, during the late Pleistocene all these species were distributed from Florida north to Virginia. A transition to the “north-east province” occurred in Virginia, as evinced by the

presence of “northeastern” index species cited by FAUNMAP (1996). Thus, a “southeastern province” would include Georgia and the Carolinas as well as Florida.

In the United States, the 100°W meridian separated eastern and western Pleistocene vertebrate assemblages that differed broadly from each other. It follows that small mammal species that occur in Florida but not in Virginia may also define the western limits of the “southeastern province.” Possible candidates might be *Geomys pinetus*, *Peromyscus polionotus*, *Neofiber alleni* and *Sylvilagus palustris* (see Table 3; Brown, 1997). Northern ungulates (*Bootherium bombifrons*, *Cervalces* sp., *Rangifer tarandus*) occur sporadically in late Pleistocene deposits scattered between north-western Alabama and north-eastern Texas (Churcher *et al.*, 1989; McDonald & Echols 1990; George Phillips, personal communication 2006), accompanied by turtles (*Clemmys insculpta*, *Emydoidea blandingii*) that presently live north of the Ohio-Missouri rivers (Phillips, 2006). These occurrences suggest that cool temperatures driven by katabatic winds may have displaced warm-adapted vertebrate associations to lower latitudes west of the Southern Appalachians than in the postulated thermal enclave to the east. As noted above, the Southeastern enclave may have been somewhat sheltered from these winds by the mountains, which locally rose to elevations comparable in height to the LGM ice sheet occupying the Great Lakes region (approximately 2,000 m; Dyke *et al.*, 2002).

Comparisons of Southeastern vertebrate assemblages with the coeval assemblage from the Rancho La Brea tar pits in California (Table 4) imply that during the latest Pleistocene the more fully sampled eastern states (Florida, Virginia) hosted greater vertebrate diversity than that present in coastal southern California. Georgia and the Carolinas, which are greatly under-sampled relative to tar pit collections, have nevertheless yielded assemblages of a diversity comparable to those of the tar pits. In support of the zoogeographic findings of FAUNMAP (1996), the vertebrate assemblage from the California site is less similar to that of Florida than is the assemblage from the northern Great Lakes region. Interestingly, the similarity between eastern North American and western North American (Yukon) mammalian carnivoran assemblages is greater than in most other eastern and western clades of non-avian vertebrates (Table 5). Elevated terrain need not have posed a significant barrier to the transcontinental dispersal of the largest mammalian herbivores. Remains of *Mammuthus americanum* have been recovered from an altitude of about 900 m (Garton 1992) and those of *Mammuthus columbi* from about 2,800 m (Gillette 1996; Graham, Weis & Holen, 2003). The high rate of mammalian extinction in California corresponds to its position on the latitudinal extinction gradient suggested here for the eastern United States (Table 4).

Large herbivores must have been affected by changes in the distribution of their preferred food resources. In Siberia, Ukrainseva (1993; see also Geel *et al.*, 2008) identified 221 cryptogams and flowering plants in frozen gastrointestinal contents of *Equus* spp., *Bison* spp., and numerous specimens of *Mammuthus* spp. The animals fed on herbs and mosses wherever they were abundant. Trees and shrubs were also browsed, but not extensively. She concluded that the “mammoth fauna complex” became extinct in Eurasia as climates

became warmer and wetter, and the quality and abundance of forage declined. Conversely, it must be noted that mammoth populations apparently increased during the mid-Holocene on Wrangel Island off north-eastern Siberia, with the northward expansion of warmer, subarctic vegetation (Vartanyan *et al.*, 2008). In the Beringian region to the east, evidence preserved in various environments, including the gastrointestinal contents of large vertebrates, suggests that a “mammoth steppe” was dominated by dry-facies grasses (Zazula *et al.*, 2003). In the same region, *Ursus* spp., *Equus* spp., and *Bison* spp. populations began to show the effects of climatic stress with the onset of the Wisconsinan LGM as floral diversity declined (Willerslev *et al.*, 2003), apparently before the arrival of human hunters (Barnes *et al.*, 2002; Guthrie, 2003; Shapiro *et al.*, 2004; but see Buck & Bard, 2007). Sergei Zimov (in Stone, 1998) hypothesized that during the late Pleistocene Arctic grasslands were maintained through the churning of soils by the feet of large vertebrates.

In view of the long-sustained tempo of alternating glacial and interglacial intervals throughout the Pleistocene, it is difficult to accept that climatic change alone was the major factor in generating the terminal Pleistocene extinctions. The Wisconsinan megafauna survived the early phases of deglaciation, when continental ice was retreating to the north at approximately 100 m per year and the strand line of the Southern Atlantic Bight was simultaneously advancing westward across the coastal plain at about 10 m per year. In the FAUNMAP (1996) “northeastern province,” which was severely impacted by climatic change, mammalian extinctions were of the order of 20%, whereas in Florida, where climatic changes were comparatively minor, extinction levels approached 40% (Table 4; Holman, 2001; see also Webb & Simons, 2006). Extinction levels were similarly high in California, where several megafaunal species also inhabiting Florida were present. These species evidently accommodated a flora that differed from that of Florida to a greater extent than glacial and postglacial floras within Florida differed from each other (Thompson & Anderson, 2000; Williams *et al.*, 2000). It seems unlikely that, even in combination, climatic and vegetational changes were responsible for the postglacial extinction of megafauna throughout North America. Weir & Schluter (2007) have shown that rates of extinction (and speciation) of birds and mammals are typically faster at high latitudes where species diversity is low, than at low latitudes where species diversity is high. The reverse pattern is suggested by the Pleistocene megafaunal extinctions, implying they may have resulted from atypical (e.g. human-induced) forcing factors.

We are thus left confronting the long and spirited debate on the role of humans in the terminal Pleistocene extinctions (Barnosky *et al.*, 2004). Indeed, recent spore and charcoal analyses in the adjacent FAUNMAP (1996) Northeastern Faunal Province imply that megaherbivore dung deposition declined as anthropogenic charcoal levels increased prior to the beginning of the terminal Pleistocene (Younger Dryas) cold interval (Robinson *et al.*, 2005). This has been interpreted as evidence of a collapse in large mammal herbivore populations following the arrival of proficient human hunters. It has also been suggested that the lack of efficient dispersal agents for certain trees with

large fruits (*Asimina triloba*, *Gleditsia triacanthos*, *Gymnocladus dioica*, *Maclura pomifera*) points to the former presence of megafaunal vectors (Barlow, 2000). In addition to climatic shifts, the abatement of megafaunal browse on plant formations (Whyte *et al.*, 2003) during the Pleistocene-Holocene transition and the diminished role of fire may also have promoted the expansion of forested environments (Barden, 1997). In cognizance of contrasting opinions relating to the influence of humans on Pleistocene faunal extinctions, we refer readers to alternative interpretations presented in Grayson & Meltzer (2003, 2004) and Fiedel & Haynes (2004).

VIII. BIOHISTORICAL IMPLICATIONS

As noted previously, the generic-level extinction rate for large mammals in North America through the last 1.7 ma of Pleistocene time was comparable to that of terrestrial mammals in general through Cenozoic time, despite the occurrence of at least 27 peak glacial and interglacial cycles (Alroy, 1996; data in Martin, 2005; and see pg. 2 of Raymo *et al.*, 2004). Thus, previous to the terminal Pleistocene extinctions, the survival of large mammalian species had not been unusually threatened by rapid climatic change. It has been estimated that each origination of terrestrial species of plants, insects, and aquatic and terrestrial vertebrates typically requires 1-2 ma (Hewitt, 2000). Accepting this estimate, the 20,000 years since the LGM would have represented 1-2% of the time necessary for speciation. The level of postglacial genomic change in Europe supports this inference, remaining at a subspecies or molecular level through the interval (Hewitt, 2000; Schmitt, 2007). Because ice sheets were more extensive and persisted longer in North America (Hawkins & Porter, 2003), it is likely that postglacial environmental forcing of genomic change in North America was less than in Europe. However, strategies for survival placed a premium on change of location rather than adaptation on both continents (Martínez-Meyer *et al.*, 2004; Waltari *et al.*, 2007). That postglacial expansion of temperate species was greatly facilitated by the survival of small populations in small temperate enclaves (“cryptic northern refugia”) scattered through the tundra in proximity to continental glaciers was initially recognized in Europe (Stewart & Lister, 2001; Valdósera *et al.*, 2007). The presence of one such refugium has been documented in the north-central United States; it remained unglaciated during the LGM (“driftless” region of Wisconsin), and supported deciduous vegetation and small rodents similar to those in the Southeast (Rowe *et al.*, 2004).

The Southeast was to a substantial degree isolated during the LGM. The diverse biota (Hewitt, 2000) of the enclave as described here occupied about 550,000 km² (approximating the area of Iberia; Gómez & Lunt, 2006) south-east of the Appalachian Mountains. The enclave was located on an unglaciated terrain that extended south of the glacial front over approximately 10,500,000 km² (or about the area of Europe), but the enclave occupied only about 5% of the

terrain's area. To the west of the continental ice sheets extended Beringia, an arctic but largely unglaciated terrain that covered about 34,000,000 km² (Brubaker *et al.*, 2005), or three times the area of unglaciated southern North America. During the LGM, contacts between Beringia and the unglaciated south were tenuous, essentially limited to a slender unglaciated "isthmus" extending along the north-west coast of the continent (Hetherington *et al.*, 2004; Cook *et al.*, 2006). After 12,000 cal y BP, and following the postglacial rise of sea level that separated eastern and western Beringia, an "ice-free corridor" began to open between the Cordilleran and Laurentian ice sheets. The corridor was simultaneously colonized by Beringian biota from the north, and southern North American biota from the south. "Cryptic northern refugia" surely played a major role in facilitating the rapid merger of biota from Beringia and southern North America (Jackson & Wilson, 2004; Rowe *et al.*, 2004; Brubaker *et al.*, 2005; Anderson *et al.*, 2006). When the "ice-free corridor" opened to the north, the potential role of the thermal enclave in the Southeast, hitherto sheltered behind the biogeographic barrier of the Appalachians (Delcourt, 2002; Ibáñez *et al.*, 2006), was probably muffled by the severe extinctions that occurred within it (Table 4)

It is evident that terrestrial biota possesses an ability to recover from sudden and dramatic regional changes in climate that might otherwise produce mass extinctions (Barnes *et al.*, 2002; Guthrie, 2003; Shapiro *et al.*, 2004). Following the LGM, global temperatures increased sharply, subjecting North America to an epoch of rapid global warming. Some 55 ma previously, global climates also underwent a dramatic warming, but within a higher range of temperatures. During the approximately 220,000 years of the Paleocene-Eocene thermal event, polar sea levels rose about 5 m and polar climates became subtropical. North America was entirely free of ice. During summer months the Arctic Ocean was capped by a sheet of fresh water in which floating ferns flourished (Brinkhuis *et al.*, 2006; Sluijjs *et al.*, 2006). No associated extinctions occurred across North America, but, as during warm episodes of the Pleistocene, plants and animals immigrated into the continent across newly warm high-latitude isthmuses (Harrington, 2001; Bowen *et al.*, 2002; Alroy, 2003). Within 10,000 years mid-latitude floras were displaced approximately 1,000 km to the north, as mean annual temperatures rose by 5°C (Wing *et al.*, 2005). Plant communities were enriched and restructured on a species-by-species level by immigration. Were it not for the possibility of human involvement in the post-LGM warming, the two thermal forcing events, one Pleistocene (cold) and the other Palaeogene (warm), could easily have been fitted into a single gradient of "global warming" (*cf.* Wing, 2007).

IX. CONCLUSIONS

(1) Although data relating to the Pleistocene thermal enclave north of Florida are currently meagre, it is apparent that a warm, mesic biota extended beyond Florida, and may have exhibited local biogeographic detail (*cf.* "refugia within refugia"; Gómez & Lunt 2006).

(2) The existence of a late Pleistocene thermal enclave bound by the Southern Appalachians to the west and the Atlantic coast to the east is suggested by physical environmental evidence. Despite their proximity to the LGM glacial front, the Southern Appalachians were not glaciated. Ground water palaeotemperatures reflect cold climates in Maryland immediately north of the enclave, and warm mesic climates within it in Georgia. Prevailing LGM coastal wind directions may have been similar to or stronger than those at present, and a strong Gulf Stream closely paralleled the coast from Florida north as far as Cape Hatteras at latitude 35°N in North Carolina.

(3) The presence of a thermal enclave seems well-supported by biological evidence. Plants and vertebrates characteristic of Floridian biota were also distributed across the region between the Appalachians and the Atlantic north to Cape Hatteras. The "Southeastern" FAUNMAP (1996) province extended from Florida to the southern border of Virginia, where it met the "Northeastern Province" in turn juxtaposed to the Wisconsinan glacial front. Vertebrate abundances, exemplified by the replacement of the heat-tolerant *Mammuthus columbi* by the cold-adapted *M. primigenius*, suggest that substantially cooler climates prevailed in Virginia than in the enclave immediately to the south. Insectivores, rodents and artiodactyls were more typical of the Virginian fauna, whereas turtles, lizards and edentates were more diversified in Florida. The gradient separating warm and cool temperatures north of Cape Hatteras was probably steep. A much shallower gradient extended from the Cape south to Florida, wherein evidence of prairies and prairie-adapted vertebrates increased as that for forests and forest-dwelling vertebrates dwindled. The gradient is exemplified by the gradual southward replacement of *Mammuth americanum* by *Mammuthus* spp. as the most commonly recorded proboscidean. A similar ecotone probably existed from the highlands of the Southern Appalachians east towards the low country bordering the Atlantic coast.

(4) Patches of prairie were widespread throughout the enclave prior to the late Pleistocene megafaunal extinction. The abundant and diversified presence of grazing mega-herbivores probably inhibited the regeneration of trees and shrubs and favoured the extension of grasslands (Whyte *et al.*, 2003). During the extinction interval, which may have lasted on the order of a millennium south of the waning glacial front, extirpation was more frequent in Virginia whereas extinction was more common in Florida. Small vertebrates were little affected by extinction. Ectothermic amphibians and reptiles tended to remain within their LGM ranges, but surviving endothermic birds and mammals tended to follow plant biomes to the north and west, into deglaciated terrain beyond the limits of the enclave. Prairies probably waned within the Southeast, the FAUNMAP (1996) Southeastern and Northeastern faunal provinces merged, and the enclave disappeared.

(5) The variety of plants and animals of the south-eastern thermal enclave provides information relating to the biogeography of ice-age North America, and the importance of the enclave within the continent. Plant and mammal species tended to persist throughout the Pleistocene, altered their ranges at similar rates, and were

interlinked. Both formed transient associations (“biomes” or “provinces”) according to their individual niche requirements, the species composition of which changed over millennial timescales during postglacial periods. Low-level, long-enduring levels of group preference have been identified among mammals. This finding is supported by the partial separation of fauna into species preferring prairie and those preferring forest habitats, reflecting a tendency among vertebrates to associate with particular plant biomes.

(6) Because the glacial segment of the Pleistocene climatic cycle endured much longer than the interglacial segment, the glacial configuration of biotic associations was probably more characteristic of the Pleistocene period than the interglacial one. A regime of alternating climates also implies that a south-eastern thermal enclave probably appeared and disappeared repeatedly throughout the Pleistocene (for high-latitude floral alternations, see Muhs *et al.*, 2001, and Willerslev *et al.*, 2007). Available information suggests that megafaunal species tended to be more broadly distributed across the continent than plant species, and that megacarnivore species were most widely distributed. Nevertheless species of both guilds ranged far to the north and south of the mid-continental glacial front. Neither the Appalachians nor the Rockies imposed insurmountable barriers to the distribution of large mammals.

(7) The presence of cold-adapted megafaunal species in southern midcontinental lowlands suggests that the region may have been cooled by katabatic winds blowing from the ice front located to the north. East of the Appalachians, the replacement of a sharp ecotone defining the northern limit of the south-eastern thermal enclave by gradual environmental gradients to the south implies that the effects of proximity to continental ice dwindled rapidly with distance. It is likely that Pleistocene plants and animals avoided regions of low plant productivity. However the existence of subtropical and boreal prairies inhabited by diverse assemblages of large mammals suggests that temperature was less important than low productivity (e.g. presence of perennial ice) in limiting large mammal distributions.

(8) Communities of large grazing mammals evidently prospered in regions too cold to support forests. The south-eastern thermal enclave supported forests as well as prairies, and abundant fodder for both browsing and grazing megaherbivores. Mammalian diversity was perhaps greater in the enclave than in more homogeneous environments. The latter probably included spruce-dominated wetlands south of the glacial front (Shapiro *et al.*, 2004), fire-prone coastal brushlands in California (Stock & Harris, 2001), and semiarid grasslands of the south-western United States (Morgan & Lucas, 2005). The more mesic Southeastern enclave may have accordingly constituted a centre of late glacial biodiversity in the Americas north of Mexico.

(9) As noted above, the cause or causes of the terminal Pleistocene megafaunal extinctions are beyond the scope of this work. However, the event does persuade us to list some of its more peculiar ecological attributes. It would seem that the megafauna survived the rigours of repeated climatic cycles only to be exterminated at the end of one otherwise “uninteresting” cycle when climates were moderating from

full glacial conditions. Nearly all of the species of plants and small vertebrates that survived remain alive today.

(10) Megafaunal extinctions appear to have been more severe in southern latitudes where climates were relatively benign, and less severe in northern latitudes where climates were relatively harsh. It has been observed (Barnes *et al.*, 2002; Guthrie, 2003; Shapiro *et al.*, 2004) that megafaunal populations were becoming stressed north-west of the continental icecap during the interval leading to the LGM. Evidence of stress in megafaunal populations south of the glacial front in the United States appears to be postglacial and associated with the presence of *Homo sapiens* (Robinson *et al.*, 2006; Webb & Simons, 2006). Conversely, floral changes north-west of the glacial front were profound (Zazula *et al.*, 2007), whereas those to the south were minor relative to the amplitude of megafaunal extinctions. A few plant species, either dependent on megaherbivores for seed dispersion (Barlow, 2000) or to suppress competition from woody plants, suffered range restrictions.

(11) The North American megafauna occupied niches similar to those preferred by living megafauna in Eurasia and Africa. In North America several floral niches that apparently supported extinct megafauna survived the Pleistocene (Martínez-Meyer *et al.*, 2004). Surviving megafaunal populations tend to prosper and proliferate rapidly in situations that are inimical to the presence of humans (Bengis *et al.*, 2003; Martin, 2005; Mycio, 2005).

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