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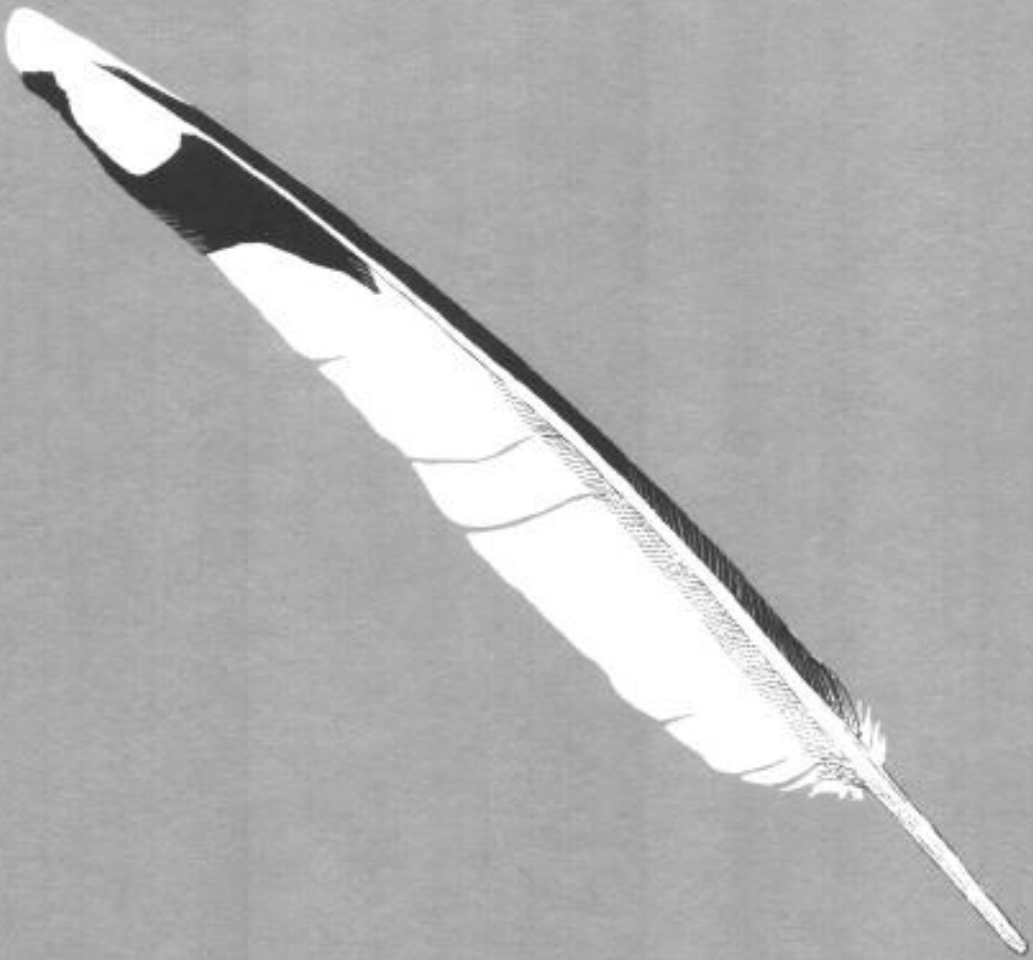

Avian Community, Climate, and Sea-Level Changes in the Plio-Pleistocene of the Florida Peninsula

by

Steven D. Emslie

AVIAN COMMUNITY, CLIMATE, AND SEA-LEVEL CHANGES IN THE PLIO-PLEISTOCENE OF THE FLORIDA PENINSULA

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AVIAN COMMUNITY, CLIMATE, AND SEA-LEVEL CHANGES IN THE PLIO–PLEISTOCENE OF THE FLORIDA PENINSULA

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ABSTRACT.—Eleven previously unidentified fossil avifaunas from Pliocene and Pleistocene localities in the Florida peninsula are presented, within which are included the description of a new species of anhinga (*Anhinga beckeri*), woodcock (*Scolopax hutchensi*), and pygmy-owl (*Glaucidium explorator*), and a new genus and species of condor (*Aizenogyps toomeyae*). The paleospecies *Milvago readei, Dorypaltus prosphatus,* and *Protocitta dixi* are considered to be synonymous with the living taxa *Milvago chimachima, Vanellus chilensis,* and *Pica pica,* respectively. These 11 avifaunas supplement the existing record of fossil birds from Florida that collectively provide a unique chronology of originations and extinctions of 239 extinct and extant taxa during a climatically dynamic period that began approximately 2.5 million years ago (Ma). Topographic and bathymetric maps of the peninsula are used with Geographic Information Systems software to model and correlate sea-level changes with the location and age of major fossil sites, the avian chronology, and presumed primary habitat of each represented taxon. These analyses indicate range expansions of Neotropical, western North American, and continental forest birds into the Florida peninsula during glacial stages, and the isolation, extirpation, or extinction of many of these taxa during interglacial stages. The relatively rapid climatic cycles of the Plio–Pleistocene, combined with the low topography of the peninsula, caused significant loss of wetland habitat during interglacial marine transgressions, especially in southern Florida. This habitat reduction probably accounted for extinctions of many wetland birds, especially those with relatively small body-size, in the late Pliocene. Additional extinctions recorded in the early Pleistocene resulted in a gradual loss of species richness in these communities by the end of the Pleistocene, when modern wetlands were established. Climatic events in the Pleistocene influenced terrestrial communities with the periodic formation and fragmentation of the Gulf Coast corridor, a mosaic of dry, thorn-scrub, savannah, wetlands, and hammocks, that united Neotropical regions to the south with western North America and the Florida peninsula. This corridor developed with the emergence of the shallow continental shelf in the Gulf of Mexico during glacial stages, which in some cases more than doubled the land area of the peninsula and allowed numerous species of mammals, birds, reptiles, and plants to extend their ranges into Florida. Fragmentation of this corridor during interglacial stages caused loss of species richness, probably from loss of habitat heterogeneity in the peninsula. Unlike wetland communities, modern terrestrial communities did not develop until the early Holocene, after the last fragmentation of the corridor and extinction event at 0.01 Ma. Fossil passerine remains suggest that North American continental migration patterns began developing in the peninsula in the late Pliocene, and were fully established by the late Pleistocene, but Neotropical migration patterns may not have developed until the early Holocene. The chronology presented here provides a model of avian biogeography and community development in the Florida peninsula during the ice ages that can be tested with future paleontological research.

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Those who are unfamiliar with the geology of Florida are often surprised to learn of the excellent fossil record of vertebrates known from this state. This record includes the most complete chronology of extinct and extant birds in the Neogene of North America. The avian record beginning 2.5 million years ago (Ma), from the initiation of the ice ages in the late Pliocene to the end of the last major glaciation (the Wisconsinan) in the late Pleistocene at 0.01 Ma, is particularly well known from dozens of localities that span this period and from the extensive research that has been completed on fossil birds in Florida by Dr. Pierce Brodkorb and his students since 1952 (see Campbell 1992). This monograph is a culmination of more than 14 years of research by the author on Plio–Pleistocene birds in the Florida peninsula. Here, I present the systematic paleontology of avifaunas recovered from four new and seven previously described fossil localities that includes the description of one new genus and four new species, and the identification of 23 extant and three extinct species previously unreported as fossils from Florida.

I use this extensive addition to Florida's fossil record with data from numerous previously published avifaunas, with certain modifications, to develop a 2.5 million-year chronology of extant and extinct birds in the peninsula. I compare this avian chronology with the glacial and interglacial stages that caused sea-level changes during the Plio–Pleistocene to discern patterns in avian originations and extinctions during this climatically dynamic period. Geographic Information Systems (GIS) software (Idrisi 1.01, Clark Univ., Worcester, MA) is employed to model sea-level changes in the peninsula during five time periods from 2.5 to 0.01 Ma. Patterns in these originations and extinctions, based on probable habitats occupied by these birds, are inferred from these comparisons to develop a model of avian historical biogeography and community development during the Plio–Pleistocene. My primary hypothesis here is that, because of its low topography and geography, the Florida peninsula was subject to relatively frequent and rapid changes in land area during the ice ages when even minor sea-level changes (1 m or less) impacted this region. As I will demonstrate below, these changes over the past 2.5 Ma had a significant influence on the composition of avian communities in the peninsula where modern communities developed only recently. This model can be tested and refined with future additions to the fossil record of Florida. The model also may prove beneficial for estimating future changes to avian communities in the Florida peninsula in conjunction with other climate models on this region (e.g., Box et al. 1993).

METHODS

Systematic analyses and comparisons of fossil material were completed at the Florida Museum of Natural History, Gainesville (FLMNH), the U.S. National Museum of Natural History, Washington, D.C. (USNM), the University of Michigan Museums of Paleontology (UMMP) and Zoology (UMMZ), Ann Arbor, the American Museum of Natural History, New York (AMNH), and the Natural History Museum of Los Angeles County (LACM). Terminology follows that of Howard (1929). Most fossil specimens reported here are catalogued with University of Florida (UF) numbers, or with UF/PB numbers for specimens originally in the collection of Pierce Brodkorb. All measurements were taken with digital calipers, rounded to the nearest 0.1 mm.

Excavations were conducted at two fossil localities (Haile 7C and Inglis 1C, see below) to obtain additional avian fossils, and to collect paleomagnetic and pollen samples for chronological and paleoecological information. Pollen samples were collected from in situ, bone-bearing sediments and natural stratigraphic layers using sterile whirl pacs and a clean trowel; paleomagnetic samples also were collected from in situ sediments at Haile 7C, Inglis 1C, and the De Soto Shell Pit. Additional pollen samples from Inglis 1A, McLeod Limerock Mine, and Reddick 1A were extracted from sediments archived in the collections at AMNH and FLMNH. Pollen samples were prepared and analyzed by F. Rich, Georgia Southern University. B. MacFadden (FLMNH) collected the paleomagnetic samples from Haile 7C and Inglis 1C.

The chronology of avian originations and extinctions in the Plio–Pleistocene of Florida was constructed by placing fossil taxa within one or more time periods based on their fossil record. Five time periods were chosen for this analysis following those distinguished by Harland et al. (1990) and Morgan and Hulbert (1995), with some modification, for major fossil localities in Florida based on vertebrate biochronology, biostratigraphy, and geochronology. These time periods (and their corresponding North American Land Mammal Age given in parentheses) are the late Pliocene (late Blancan; 2.5–2.0 Ma), latest Pliocene (early Irvingtonian; 2.0–1.6 Ma), early Pleistocene (late early Irvingtonian; 1.6–1.0 Ma), late early and middle Pleistocene (middle to late Irvingtonian; 1.0–0.3 Ma), and late middle and late Pleistocene (Rancholabrean; 0.3–0.01 Ma). In this chronology, Haile 7C is included with latest Pliocene sites, although Morgan and Hulbert (1995) consider it to be the only Florida locality that dates to the latest Blancan at about 2.0 Ma (Table 1). The vertebrate fauna from this site (see below), especially birds and mammals, includes taxa also identified at Inglis 1C. This latter site is considered to be similar in age to Inglis 1A and all are placed within the latest Pliocene. In addition, McLeod Limerock Mine probably dates to between 0.8 and 0.6 Ma and Coleman 2A and 3C are slightly younger at approximately 0.6–0.3 Ma (Morgan and Hulbert 1995). These sites were combined here into the middle Pleistocene period to simplify the analyses.

The avian chronology includes only those extinct and extant taxa with a fossil record in Florida. The chronology was developed from systematic data presented here and from previously published avifaunas in Wetmore (1931), Brodkorb (1953, 1956a, b, 1957, 1959, 1963a, b, 1964, 1967, 1971, 1978), Holman (1959), Woolfenden (1959), McCoy (1963), Hamon (1964), Ligon (1965), Campbell (1976, 1980), Steadman (1976, 1980, 1984), Ritchie (1980), Becker (1985a), Emslie (1988a, 1992, 1995a, b, 1996), Young and Laerm (1993), and Emslie and Morgan (1995). Several fossil taxa were not included in the analysis as they are of questionable validity and probably represent living species. These taxa include *Podilymbus wetmorei* Storer 1976 (= *P. podiceps*; see Steadman 1984), *Anas itchtucknee* McCoy 1963 (= *Anas* sp.; see Campbell 1980), and *Gallinula brodkorbi* McCoy 1963 (= *G. chloropus*; see Olson 1974 and Campbell 1980). In addition, certain taxa identified only to genus may represent species already in the chronology and were not considered separately in quantifying origins and extinctions by major time periods. These taxa include *Egretta* sp., *Eudocimus albus* or *E. ruber, Rallus elegans* or *R. longirostris,* and *Meleagris* sp. The chronological range of each taxon in Florida was assumed to be continuous across

TABLE 1. Major Plio–Pleistocene localities in Florida with their age (epoch and North American Land Mammal Age), number of avian taxa, and number of extinct taxa known from each. References are those on avifaunas only; those on other vertebrates from each site are not listed. See Morgan and Hulbert (1995) for detailed discussion on the age of most of these localities.

Localities by age	No. avian taxa	No. extinct taxa	References
Late Pliocene (late Blancan; 2.5–2.0 Ma)	46		
Macasphalt Shell Pit		13	Emslie 1992
St. Petersburg Times Site	9	2	Emslie 1992
Sante Fe River 1B	7	1	Brodkorb 1963a
Haile 15A	7	1	Campbell 1976
Richardson Road Shell Pit	11	5	Emslie and Morgan 1994; Emslie 1995b; Emslie et al. 1996
Late Pliocene (latest Blancan; ca. 2.0 Ma)			
Haile 7C *	15	4	
Latest Pliocene (early Irvingtonian; 2.0–1.6 Ma)			
Inglis 1A*	61	9	Steadman 1980; Carr 1981
Inglis 1C*	27	4	
De Soto Shell Pit 5*	6	1	
Forsberg Shell Pit*	7	3	
D&M Shell Pit*	10	3	
Pelican Road Shell Pit*	7	3	
Early Pleistocene (late early Irvingtonian; 1.6–1.0 Ma)			
Leisey Shell Pit*	49	16	Emslie 1988a, 1995a
Shell Materials Pit*	3	1	
Haile 16A*	30	2	Steadman 1980; Emslie 1988a
Payne Creek	10	1	Steadman 1984
Middle Pleistocene (middle Irvingtonian; 0.8–0.6 Ma)			
McLeod Limerock Mine, Pocket A*	7	2	
Middle Pleistocene (late Irvingtonian; 0.6–0.3 Ma)			
Coleman 2A and 3C*	36	5	Ritchie 1980; Steadman 1980
Late Pleistocene (late Rancholabrean; 0.13–0.01 Ma)			
Reddick 1A*	54	8	Brodkorb 1957; Hamon 1964; Steadman 1976
Arredondo 2A	42	3	Brodkorb 1959; Steadman 1976
Ichetucknee	64	4	McCoy 1963; Campbell 1980
Rock Springs	36	2	Woolfenden 1959
Haile 11B	71	4	Ligon 1965
Cutler Hammock*	51	5	Emslie and Morgan 1995
Lecanto 2A*	24	0	Morgan 1991
+Sixteen other localities	59	2	Lundelius et al. 1983

* Localities for which analyses of all or part of the avifauna are presented in this paper.

gaps between known fossil occurrences. It is possible, however, that some species periodically were extirpated and reinvaded the peninsula, although the record is too coarse to recognize such patterns. In addition, the term "origination" is hereafter used to refer to first appearances of taxa in the fossil record of Florida and does not necessarily indicate speciation events (although some species, including the Florida Scrub-jay [*Aphelocoma coerulescens coerulescens*], do appear to have evolved in Florida; see Emslie 1996). The term "extinction" is used to refer to disappearance of taxa from the Florida fossil record. Aside from true extinction, this term includes local extirpations of extant taxa and, in some cases, of extinct taxa that have a longer fossil record outside of Florida.

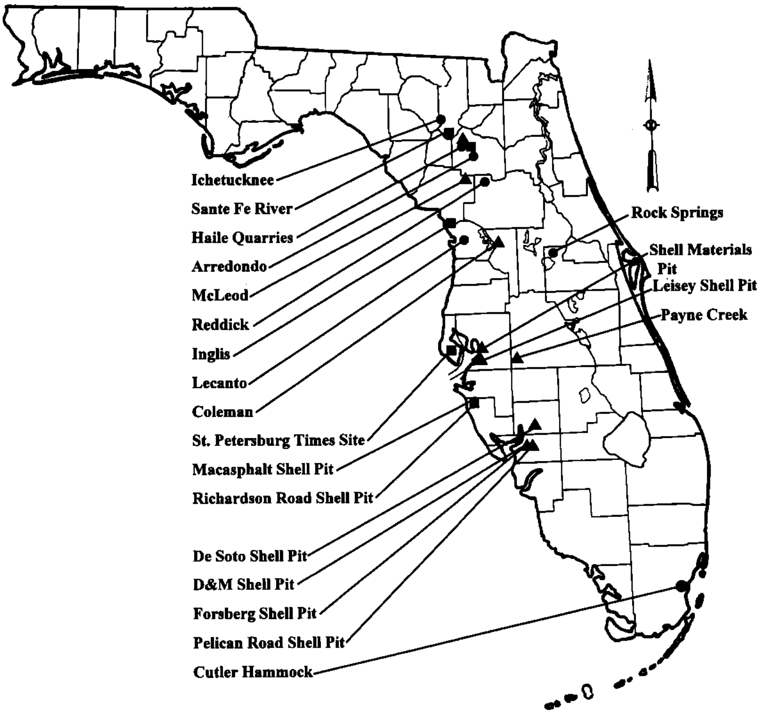

FIG. 1. Florida, showing the location and age of the major fossil localities discussed in the text. ■ = late Pliocene (late Blancan and early Irvingtonian), ▲ = early Pleistocene (Irvingtonian), ● = late Pleistocene (Rancholabrean).

General habitat requirements and current status of extant species in Florida were determined from information provided in Stevenson and Anderson (1994). Habitat requirements for extinct taxa were inferred from that of their nearest modern relatives and/or using paleoecological information from the fossil localities in which they occur. Five major habitats were selected for classification of fossil taxa: (1) dry thorn-scrub, grassland, or savannah; (2) subtropical forest and mesic hammock; (3) North American continental pine and deciduous forests; (4) freshwater aquatic and semiaquatic; and (5) coastal and marine. In cases where a single taxon could occupy more than one of these habitats, the primary habitat in which it or its modern counterparts is most often found was used in the habitat analyses. Variation in origins and extinctions by habitat and time period was analyzed using chi-square goodness-of-fit tests ($P < 0.05$). The GIS analyses were completed with Idrisi software (Clark Univ., Worcester, MA) and by overlaying bathymetric and topographic maps of the Florida peninsula, hereafter defined as that area of the state below 30°N latitude, and the Gulf of Mexico to model sea-level changes at 1-m and 10-m intervals. Land area lost/gained with sea-level change was calculated using the Idrisi program.

SITE DESCRIPTIONS AND PALEOECOLOGY

The fossil localities include riverine, sinkhole, and marine shell-bed deposits found throughout the Florida peninsula (Fig. 1) and range in age from late Plio-

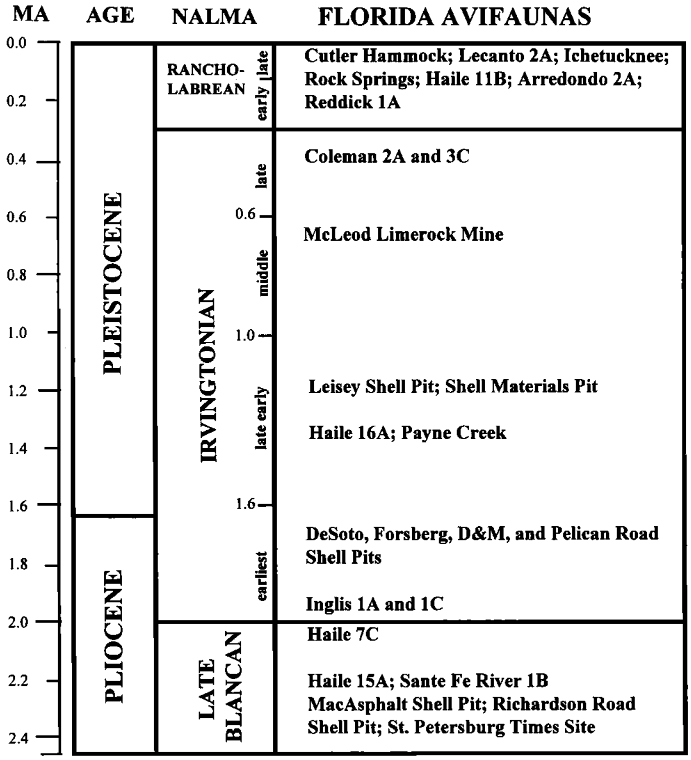

FIG. 2. Stratigraphic chart of localities with fossil avifaunas in the Florida peninsula in correlation with North American Land Mammal Ages (NALMA). Time scale is in millions of years ago (Ma).

cene to late Pleistocene (Fig. 2). Each site has produced small to large collections of fossil vertebrates, including birds (Table 1). Most of the sites discussed here have been described in other publications; except for Inglis 1C, these data are summarized by Morgan and Hulbert (1995) and need not be repeated here. A brief description of those localities from which new fossil avifaunas are reported is presented below. A summary of the avian taxa identified from each site is provided in Tables 2 and 3.

HAILE 7C

Haile 7C was discovered in 1989 during limerock mining operations at the Haile quarries, Alachua County, north-central Florida. The site was excavated initially by personnel from FLMNH in 1989–1990. A rich mammalian fauna was recovered that represents at least 16 taxa, including a pampathere (*Holmesina floridanus*), an undescribed species of giant ground sloth (*Eremotherium* sp.), and an undescribed species of tapir (*Tapirus* sp.). Fossil birds recovered during these excavations included a new species of tropical hawk-eagle (*Amplibuteo* sp. Emslie and Czaplewski, in press), Ringed Kingfisher (*Ceryle torquata*), and several taxa of ducks (see below). Based on the mammalian biochronology, the site is estimated to date to ca. 2.0 Ma (latest Blancan); the absence of any strictly Blancan taxa precludes determination of a more precise date (Morgan and Hulbert 1995).

In December 1994, this site was excavated by the author to recover additional

TABLE 2. Avian taxa identified from Pliocene and Pleistocene fossil localities in Florida. Numbers for each taxon refer to total number of identified elements with minimum number of individuals represented given in parentheses.*

Taxon	I1A	I1C	H7C	H16A	L2A	CH
Gavia pacifica‡	1 (1)					
Gavia immer						1 (1)
Tachybaptus dominicus	1 (1)					
Podilymbus podiceps	6 (2)		2 (1)		2 (1)	25 (4)
Podiceps sp.	2 (1)					
Podicipedidae, indeterminate	1					1
Phalacrocorax idahensis†,‡		8 (1)				
Anhinga anhinga						1 (1)
Anhinga beckeri†,§						2 (1)
Botaurus lentiginosus	1 (1)					
Ixobrychus exilis	2 (1)				1 (1)	
Ardea herodias						1 (1)
Ardea sp.	1 (1)					
Butorides virescens						1 (1)
Endocimus albus or *E. ruber*	1 (1)					1 (1)
Teratornis merriami†						5 (1)
Coragyps atratus	19 (4)			18 (4)		30 (5)
Cathartes aura					2 (1)	2 (1)
Gymnogyps californianus						15 (2)
Gymnogyps kofordi†				34 (2)		
cf. *Gymnogyps* sp.†	1 (1)					
Aizenogyps toomeyae†,§			4 (1)			
Ciconia maltha†						2 (1)
Anabernicula gracilenta†	2 (1)					
Aix sponsa	6 (1)		3 (1)			
Anas crecca					1 (1)	
Anas crecca or *A. discors*	5					
Anas platyrhynchos	2 (1)					5 (2)
Anas discors or *A. cyanoptera*			1 (1)			
Anas clypeata			2 (1)			
Anas sp.	3		3			1
Aythya sp.	1 (1)					
Bucephala albeola			1 (1)			
Mergus sp.			1 (1)			1 (1)
Oxyura jamaicensis						2 (1)
Anatidae, indeterminate			9			3
Pandion haliaetus						2 (1)
Haliaeetus leucocephala						2 (1)
Neophrontops slaughteri†,‡	11 (1)					
Circus cf. *C. cyaneus*‡				1 (1)		
Accipiter cooperii	6 (2)			1 (1)	1 (1)	4 (1)
Buteogallus urubitinga‡	1 (1)					
Buteo lineatus				1 (1)	6 (2)	12 (2)
Buteo swainsoni or *B. lagopus*						1 (1)
Buteo cf. *B. jamaicensis*						7 (3)
Buteo sp.	17			1	1	7
cf. *Buteo* sp.		1				
Amplibuteo sp.†		4 (2)	10 (1)			
Aquila chrysaetos						4 (1)
Aquila sp.†	37 (2)					
Spizaetus grinnelli†						2 (2)
Caracara plancus						30 (3)
Milvago chimachima readei‡						5 (1)

TABLE 2. Continued.

Taxon	I1A	I1C	H7C	H16A	L2A	CH
Falco sparverius	15 (3)				2 (2)	1 (1)
Falco columbarius	2 (1)					1 (1)
Falco cf. *F. peregrinus*						1 (1)
Cradidae, indeterminate†				4 (2)		
Meleagris gallopavo					2 (1)	35 (4)
Meleagris leopoldi or *M. anza*†	1,240	14 (2)	7 (2)			
Meleagris sp.				17 (1)		
Colinus virginianus	1,048			23 (3)	5 (3)	9 (2)
Laterallus cf. *L. exilis*				2 (1)	2 (1)	
Rallus elegans or *R. longirostris*	11 (3)	2 (1)			1 (1)	3 (1)
Rallus limicola				13 (3)	3 (1)	
Rallus sp. A†				3 (1)		
Rallus sp. B†	2 (2)		1 (1)			
Rallus sp.		1	1			
Porzana carolina	3 (2)				1 (1)	
Porphyrula martinica						1 (1)
Fulica americana						6 (2)
Rallidae, indeterminate	1					
Grus americana	1 (1)					
Titanis walleri†	10 (1)					
Jacana spinosa					1 (1)	
cf. *Tringa* sp.		1 (1)				
Catoptrophorus semipalmatus‡			1 (1)			
Calidris cf. *C. pusilla*‡					5 (1)	
Limnodromus scolopaceus			2 (1)	1 (1)		1 (1)
Gallinago gallinago	10 (4)	1 (1)				1 (1)
Scolopax minor						1 (1)
Scolopax hutchensi†,§	11 (2)	9 (2)		1 (1)		
Charadriiformes, indeterminate	1					1
Columba fasciata‡					1 (1)	
Columba sp.	1 (1)	2 (1)				
Zenaida macroura	39 (6)	1 (1)		4 (2)	1 (1)	28 (6)
cf. *Zenaida* sp.						1 (1)
cf. *Ectopistes migratorius*†						1 (1)
Coccyzus americanus	25 (3)					
Tyto alba	1 (1)			16 (3)		3 (1)
Otus asio	41 (4)	1 (1)		8 (2)	7 (2)	17 (4)
Bubo virginianus	11 (2)					2 (1)
Glaucidium explorator†,§	13 (2)					
Glaucidium sp.†	2 (2)					
Speotyto cunicularia	6 (2)					
Strix varia	2 (1)				1 (1)	
Asio sp.	3 (1)					
Aegolius acadicus‡					1 (1)	
Strigidae, indeterminate					1	
Ceryle torquata‡			1 (1)			
Melanerpes sp.	31 (7)			1 (1)		1 (1)
Melanerpes cf. *M. erythrocephalus*		4 (4)				
Picoides cf. *P. villosus*‡	1 (1)	3 (2)				
Colaptes auratus	10 (3)			1 (1)		1 (1)
Dryocopus sp.	1 (1)					2 (1)
Picidae, indeterminate	7	4				
Cyanocitta cristata	1 (1)					
Aphelocoma coerulescens	12 (5)					
Pica pica‡					1 (1)	
cf. *Pica pica*						8 (2)
Corvus cf. *C. brachyrhynchos*				1 (1)		8 (2)

TABLE 2. Continued.

Taxon	I1A	I1C	H7C	H16A	L2A	CH
Corvus ossifragus	5 (1)					83 (7)
Corvus sp.			1 (1)			
Corvidae, indeterminate						5
Catharus sp.		1 (1)				
cf. *Hylocichla mustelina*‡	3 (1)					
Turdus sp. A	3 (2)	6 (5)				
Turdus sp. B		4 (3)				
Turdinae, indeterminate		1				
Dumetella carolinensis‡		1 (1)				
Toxostoma rufum		1 (1)				
Vermivora cf. *V. celata*‡	1 (1)					
Cardinalis cardinalis	1 (1)	3 (2)		1 (1)		1 (1)
cf. *Passerina* sp.				1 (1)		
Cardinalinae, indeterminate		1		1		
Spizella cf. *S. pusilla*		5 (4)				
cf. *Chondestes grammacus*‡		1 (1)				
Passerculus sandwichensis	13 (6)	2 (1)		2 (1)		
Ammodramus maritimus‡	1 (1)					
Melospiza melodia‡	1 (1)			1 (1)		
Melospiza georgiana‡					1 (1)	
Zonotrichea cf. *Z. albicollis*‡		1 (1)				
Zonotrichea cf. *Z. leucophrys*‡	2 (2)	4 (4)		6 (5)		
Zonotrichia sp.	2					
Junco hyemalis‡		1 (1)		7 (2)		2 (2)
Junco cf. *J. hyemalis*	1 (1)	1 (1)				
cf. *Passerella* sp.				2 (1)		1 (1)
Agelaius phoeniceus	1 (1)			2 (1)		
cf. *Agelaius* sp.			1 (1)			
Sturnella magna	5 (3)					
Euphagus cyanocephalus‡	2 (2)					
Euphagus sp.	3 (1)					
Quiscalus mexicanus‡					1 (1)	
Molothrus ater	2 (2)			1 (1)		
Emberizinae, indeterminate		4				
Icterinae, indeterminate				1 (1)	4 (2)	
Passeriformes, indeterminate				1	15	

* I1A = Inglis 1A; I1C = Inglis 1C; H7C = Haile 7C; H16A = Haile 16A; L2A = Lecanto 2A; CH = Cutler Hammock.
† Extinct taxa.
‡ First fossil record from Florida; *Vanellus chilensis* from Arredondo 2A also is included in this category (see text).
§ New species described in this paper.

avian fossils and to obtain a series of paleomagnetic and pollen samples from the stratigraphic layers in the sinkhole (Fig. 3, top). Approximately 1.5 m of overlying sterile, dark brown and gray clays were removed from the surface of the site with a backhoe. The exposed bone-bearing layers of orange, gray, and yellow sands and clays were excavated with hand tools to locate and recover vertebrate fossils. The deposits extended at least 10–15 m east to west, and for at least 6–8 m north to south before overburden again precluded an exact determination of their total extent. Fossils were excavated from the top 1–2 m of exposed sediments. Plaster jackets were used to remove fossil specimens to prevent breakage and loss of associated material; the jackets were prepared at FLMNH where the specimens are curated. Sediments were not screened for microfauna; fine-mesh screens were used in this manner during the 1989–1990 excavations, but little or no microfauna was recovered (Morgan and Hulbert 1995) and continued use of this method was

TABLE 3. Avian taxa identified from early Pleistocene (Irvingtonian) fossil localities in Florida. Numbers for each taxon refer to total number of identified elements, with minimum number of individuals represented in parentheses.*

Taxon	DSP5	SMP	RPSH	FSP	DMSP	MLM
Gavia immer			1 (1)			
Gavia concinna†				1 (1)		
Podilymbus podiceps			3 (2)	1 (1)	3 (1)	1 (1)
Phalacrocorax cf. *P. auritus*				2 (1)		
Anhinga anhinga					2 (1)	
Anhinga beckeri†,‡					4 (1)	
Ardea herodias		1 (1)				
Butorides virescens	1 (1)					
Eudocimus leiseyi†				1 (1)	1 (1)	
Coragyps atratus						8 (3)
Ciconia maltha†	1 (1)		3 (2)	3 (1)	1 (1)	1 (1)
Aix sponsa	1 (1)					
Anas crecca	1 (1)				1 (1)	
Anas crecca or *A. discors*	1 (1)					
Anas clypeata					1 (1)	
Anas sp.			2 (1)			
Aythya sp.				1 (1)	1 (1)	
Bucephala albeola					1 (1)	
Lophodytes cucullatus		1 (1)				
Buteogallus fragilis†,§			1 (1)			
Buteo lineatus	1 (1)					
Buteo sp.						1 (1)
Amplibuteo woodwardi†						10 (2)
Meleagris sp.						3 (1)
Colinus virginianus						
Fulica americana			4 (2)	3 (2)	3 (2)	
Grus sp.†		1 (1)				
Tyto alba						1 (1)

* DSP5 = De Soto Shell Pit 5; SMP = Shell Materials Pit; PRSH = Pelican Road Shell Pit; FSP = Forsberg Shell Pit; DMSP = D&M Shell Pit; MLM = McLeod Limerock Mine.

† Extinct taxa.

‡ New species described in this paper.

§ First record from Florida.

considered unnecessary. Careful excavation with hand tools was the best method for locating vertebrate fossils in the dense clay layers that characterized the deposits.

The 1994 excavations resulted in the recovery of additional, associated skeletal material of *Eremotherium* sp. and *Tapirus* sp., dozens of complete turtle shells and skeletons, and several new taxa of birds including the new genus and species of condor described below. The presence of numerous complete or partial skeletons of sloths, tapirs, and turtles in this site suggest that it was a sinkhole pond or spring that acted as a natural trap during part of its depositional history (Morgan and Hulbert 1995). Numerous impressions of leaves in the clay sediments of the site, most identifiable as *Quercus* sp. (S. Manchester, pers. comm.), suggest that the pond was surrounded by oak scrub or woodland.

Eleven pollen samples were collected throughout the stratigraphic section at the north side of the site, but analyses of these samples indicated that all were barren of pollen (F. Rich, pers. comm.). Samples subjected to paleomagnetic analyses also failed to produce reliable results (B. MacFadden, pers. comm.).

FIG. 3. The fossil sites Haile 7C (top) and Inglis 1C (bottom) during excavations. In each view, the former extent of the sinkhole is only partially visible.

INGLIS 1A

This site is a sinkhole/cave deposit discovered during excavation of the Cross Florida Barge Canal (Webb 1974). The site has produced an extensive vertebrate assemblage, of which the herpetofauna (Meylan 1982) and some mammalian taxa (*Capromeryx, Megalonyx, Sigmodon, Chasmaporthetes, Trigonictis, Erethizon, Geomys,* and *Desmodus*; Klein 1971; McDonald 1977; Martin 1979; Berta 1981; Frazier 1981; Ray et al. 1981; Wilkins 1984; Morgan et al. 1988) have been studied. Because of the presence of taxa typical of both the Blancan (*Trigonictis, Chasmaporthetes*) and Irvingtonian (*Smilodon, Lepus, Equus*) the age of this fauna is considered to be latest Pliocene (2.0–1.6 Ma, early Irvingtonian; Webb 1974; Morgan et al. 1988; Morgan and Hulbert 1995). The fauna also indicates deposition at this site during a glacial stage when sea level was lower than that of today (Morgan and Hulbert 1995).

The rich nonpasserine avifauna from this site originally was identified by D. W. Steadman (pers. comm.), with additional analyses completed by Carr (1981), but only a systematic analysis of the turkeys (*Meleagris* sp.) has been published (Steadman 1980). Carr (1981) listed more than 2,700 bones of 47 species of which 6 were recognized as undescribed extinct taxa. These included two herons (*Ardea* sp. and *Ixobrychus* sp.), a hawk (*Buteo* sp.), an eagle (*Aquila* sp.), and two owls (*Glaucidium* spp.). Of these, only the eagle (Emslie and Czaplewski, in press) and one pygmy-owl (described below) are considered to be new species. The large phorusrhacoid, *Titanis walleri,* described by Brodkorb (1963a) from a single bone from the late Pliocene Sante Fe River 1B, also is known from 11 bones at this site. In addition, the fossil assemblage includes a rich collection of passerine remains, including more than 50 partial and complete bills and mandibles (the most diagnostic skeletal elements for species identification), which are identified and described below and in Emslie (1996). These remains add new information on the paleoecology of this site and support previous interpretations by Meylan (1982), based on the herpetofauna, that habitat surrounding the sinkhole during the late Pliocene consisted primarily of oak and pine-scrub (Emslie 1996). Pollen samples extracted from sediments archived at FLMNH from the original excavations also provide new paleoecological data that support these conclusions (F. Rich, pers. comm.).

INGLIS 1C

This site, discovered by amateur paleontologists in 1994, is a sinkhole deposit ca. 5 m in diameter located in the same karst bedrock as Inglis 1A and only 1 km to the east (Fig. 3, bottom). This site was cross-sectioned during construction of the Cross Florida Barge Canal in the 1960s, during which time an unknown amount of the sediments in the sinkhole was lost. The remaining portion of the sinkhole, with its in situ sediments, was excavated by the author and students from Western State College (Gunnison, Colorado), amateur paleontologists, and personnel from FLMNH in April 1996. After removing approximately 1 m of overlying sterile sands, the bone-bearing sediments extended to a depth of 2.0–2.5 m to the bottom of the sinkhole and were excavated in two stratigraphic levels, designated as upper and lower sand, based on an arbitrary boundary at approximately 2 m in depth from present ground surface. These sediments consisted of alternating layers of white, yellow, and orange sands and clays that did not remain as recognizable units throughout the sinkhole deposits. Thus, it was not possible to excavate the sediments by stratigraphic layers and arbitrary units were designated. All excavated sediments were screened through ¼-inch (0.64-cm) and $\frac{1}{16}$-inch (0.16-cm) mesh screens in the field; quantitative samples of unscreened matrix also were transported to FLMNH to be dried, weighed, and washed through 0.64-, 0.16-, and 0.08-cm mesh screens to quantify and recover additional microfauna. This matrix was sorted for bone using low-power magnification at FLMNH and Western State College.

The west side of the sinkhole contained a large boulder more than 1 m in diameter that was not moved during excavations. The area to the west side of this boulder and extending approximately 1 m to the west edge of the sinkhole wall was designated as the West Pocket. This area of the site was particularly rich in fossils. The north wall of this pocket also exposed alternating stratigraphic units of orange and white sands. Five pollen samples were extracted from these units, numbered 1–5 from top to bottom, to a depth of 0.8 m from the uppermost unit.

The vertebrate fauna recovered from this site includes taxa also identified at Inglis 1A and/or Haile 7C and suggests a similar age for these sites. These taxa are *Holmesina floridanus, Lepus* sp., *Sylvilagus webbi, Hemiauchenia macrocephala, Platygonus bicalcaratus,* an undescribed species of *Tapirus, Smilodon gracilis, Sigmodon curtisi,* and a new species of eagle (*Amplibuteo* sp. Emslie and Czaplewski, in press). Based on these data, the Inglis 1C fauna is considered to be latest Pliocene in age (early Irvingtonian, 2.0–1.6 Ma). The paleoecology of this site differs from that of Inglis 1A in indicating the presence of a palm and dense-scrub habitat as well as prairie. This interpretation is based on the presence of avian species currently associated with such habitat (i.e., woodpeckers and passerines, including *Cardinalis cardinalis, Dumetella carolinensis,* and several thrushes; Table 2) and pollen evidence for species currently found only in midwestern and western North American prairies (*Polygala alba* and *Polytaenia nuttalli*; F. Rich, pers. comm.).

MARINE SHELL BEDS IN SOUTH FLORIDA

Vertebrate fossils recovered from marine shell beds on the Gulf Coast of south Florida include small to large collections of fossil birds. These beds were formed during marine transgressions that allowed deposition of extensive, shallow-marine shell faunas. Many of these beds currently are mined to recover crushed shell for use in construction activities or phosphates for fertilizer (Brown 1988; Hulbert and Morgan 1989). These mining activities expose the stratigraphic layers containing invertebrates and occasionally vertebrates. Some of the sites, such as Macasphalt Shell Pit (also known as APAC) have produced extensive invertebrate faunas and considerable information on the paleoecology and productivity of marine environments in the Gulf of Mexico since the early Pliocene (Petuch 1982; Stanley 1986; Jones et al. 1991; Allmon 1993; Allmon et al. 1993; Jones and Allmon 1995). This site and the Leisey Shell Pit (Fig. 1) also have produced some of the richest vertebrate faunas (including birds) known from the late Pliocene and early Pleistocene of eastern North America (Morgan and Ridgway 1987; Emslie 1988a, 1992, 1995a, b; Hulbert 1987; Hulbert and Morgan 1989; Webb et al. 1989; Hulbert et al. 1995).

Fossil avifaunas from four additional shell mines are reported herein for the first time. These sites, De Soto, Forsberg, D&M, and Pelican Road Shell Pits, are located within the Caloosahatchee Formation and are latest Pliocene (early Irvingtonian, 2.0–1.6 Ma) in age (Morgan and Hulbert 1995). A rich mammalian fauna consisting of at least 32 taxa from De Soto Shell Pit 5 provides a more precise age for this site in the early Irvingtonian, at approximately 1.8 Ma (Morgan and Hulbert 1995). Although the other shell beds have not produced a similar fauna, their age can be inferred by their general equivalence in stratigraphic position within the Caloosahatchee Formation to that of De Soto Shell Pit, and by similarities in the invertebrate faunas at each site (R. Portell, pers. comm.). One other site, Shell Materials Pit, probably dates to the late early Irvingtonian (1.6–1.0 Ma) based on the presence of *Sigmodon libitinus* in the fauna (Morgan and White 1995).

HAILE 16A

This fissure deposit is described by Ray et al. (1981) and Morgan et al. (1988). Only selected taxa have been studied from the diverse assemblage of fossil vertebrates including species of *Megalonyx* (McDonald 1977), *Trigonictis* (Ray et al. 1981), and *Sigmodon* (Martin 1979), a new species of vole (*Microtus* (*Pedomys*) *australis*; Martin 1995), species of *Geomys* (Wilkins 1984), *Erethizon* (Frazier 1981), *Desmodus* (Morgan et al. 1988), and *Meleagris* (Steadman 1980), and *Gymnogyps kofordi* (Emslie 1988a). Based on the associated fauna this assemblage dates to the early Pleistocene (1.6–1.0 Ma, late early Irvingtonian; Morgan et al. 1988; Morgan and Hulbert 1995). The site has been destroyed by mining operations.

Preliminary identification of the avifauna was completed by J. Becker, who catalogued most of the material at FLMNH. He recognized at least 21 taxa of terrestrial birds, but more than 100 bones of passerines, including 24 bills and mandibles, remained unidentified until now. This avifauna fills a gap in the early Irvingtonian between the rich Inglis 1A and Leisey Shell Pit faunas, especially for terrestrial birds. This fauna also indicates that the site formed in an open savannah or grassland environment with nearby scrub, woodland, and wetland, as reflected by the abundant fossils of turkey (*Meleagris* sp.), Northern Bobwhite (*Colinus virginianus*), rails (*Rallus* spp.), Common Barn-Owl (*Tyto alba*), and Eastern Screech-Owl (*Otus asio*). The presence of a Northern Harrier (*Circus* cf. *C. cyaneus*) and an unidentifiable cracid in particular reflect this habitat. No sediments were available from this site for pollen or paleomagnetic analyses.

MCLEOD LIMEROCK MINE

Vertebrate fossils from fissure deposits at this limerock mine were recovered by T. Galusha, AMNH, in 1941. These fossils include at least 14 taxa of mammals and 8 of birds. The mammals include *Smilodon gracilis, Tapirus haysii, Canis armbrusteri,* and *Neofiber leonardi,* all from Pocket A in the mine and indicating a middle Pleistocene age (0.7–0.5 Ma, middle Irvingtonian) for this portion of the site (Morgan and Hulbert 1995). Two other parts of the site, Pockets B and C, contained taxa restricted to the late Pleistocene and are probably Rancholabrean in age. Of these, only Pocket C had avian remains, and these were limited to nearly 200 bones of Northern Bobwhite (*Colinus virginianus*) presented below.

This site has been destroyed by mining operations. No paleomagnetic samples are available, although sediments at AMNH from the original deposits of Pocket A and C were analyzed for pollen. Unfortunately, these samples were barren of pollen (F. Rich, pers. comm.).

CUTLER HAMMOCK LOCAL FAUNA

The Cutler Hammock local fauna, Dade County, was excavated by the Florida State Historical Office under the direction of R. Carr in 1985 and 1986. This sinkhole deposit produced an enormous collection of fossil vertebrates of at least 100 taxa, including thousands of bones of small mammals, snakes, and amphibians, and hundreds of bones of large mammals, especially ungulates (*Equus* sp., *Mylohyus* sp., and *Odocoileus* sp.) and carnivores (*Canis dirus, Panthera onca, Tremarctos floridanus*) (Morgan 1991; Emslie and Morgan 1995). The mammals from this site indicate a late Pleistocene age (late Rancholabrean, 0.13–0.01 Ma; Morgan and Hulbert 1995) for most of the deposits, whereas an early Holocene archaeological component was recognized in the upper portion of the sinkhole. Taphonomic studies suggest that the site probably served as a den or feeding area for *C. dirus, P. onca,* and other carnivores in the late Pleistocene (Emslie and Morgan 1995). In addition, the sinkhole may have been a natural trap for many small vertebrates. The site appears to have formed during the last glacial stage, when sea level was lower than today, placing the site on a limestone ridge surrounded by a hardwood hammock and/or pineland with a large cave system below (Morgan 1991). Extensive grasslands and wetlands must have existed near this ridge as well. All fossil vertebrates recovered from this site are housed at FLMNH.

LECANTO 2A

In 1985 and 1986, an amateur paleontologist excavated a sinkhole deposit in Citrus County, Florida, and recovered a large number of vertebrate fossils of late Pleistocene age; most of the collection subsequently was donated to FLMNH. The large mammals from the site include *Hemiauchenia macrocephala, Palaeolama mirifica, Tapirus veroensis,* and *Tremarctos floridanus.* Of the small mammals, only the bats have been studied (Morgan 1991). The collection also includes approximately 100 avian specimens representing 24 taxa. The vertebrates represented in this site, especially the birds (see below), further indicate that it probably dates to the last full glacial stage (Wisconsinan; 0.021–0.018 Ma). This interpretation is based on the presence of northern species of birds that had extended their ranges southward into the Florida peninsula at the time deposition occurred at the site, including Band-tailed Pigeon (*Columba fasciata*), Northern Saw-whet Owl (*Aegolius acadicus*), and Black-billed Magpie (*Pica pica*), and Neotropical and southern species that had extended their ranges northward, including Gray-breasted Crake (*Laterallus* cf. *L. exilis*) and Northern Jacana (*Jacana spinosa*). These taxa, along with the mammals, also reflect a forested environment with ponds or wetlands and grassland nearby that was known to exist in north Florida during the last full glacial (Watts and Hansen 1988, 1994). Unfortunately, bones from this site, as with most late Pleistocene localities in Florida, are too leached of amino acids for radiocarbon dating.

AVIAN HISTORICAL BIOGEOGRAPHY IN FLORIDA

Prior to presenting a detailed description of fossil avifaunas from Florida, it is important to provide a review of the biogeography of modern avian communities in the Florida peninsula. This background information provides a framework in which to integrate new fossil data with GIS analyses of sea-level and climatic changes associated with avian origins and extinctions in the Florida peninsula. That climatic and sea-level changes have influenced Florida's plant and animal communities has long been recognized, especially for plants (Deevey 1949). Sherman (1957) reviews the fossil record of mammals and suggests that several taxa in south Florida probably evolved in relation to sea-level rise and isolation in that region. Subsequent studies by Webb and Wilkins (1984), Webb (1990), and Morgan (1991) demonstrate a pattern of mammalian range expansions into the Florida peninsula from northern regions during interglacial stages, and from the Neotropics during glacial stages.

Neill (1957) presents a similar model of species range expansions into north Florida (including the panhandle) and cites numerous examples of speciation in, and extinction of, plants and animals associated with sea-level changes. His analysis is probably the most thought-provoking on historical biogeography in Florida. In particular, he discusses unusual biogeographic patterns in north Florida and hypothesizes that isolation of plant and animal populations in regions of high topography during marine transgressions facilitated speciation within these populations. These formerly isolated populations have maintained their genetic identity to the present and Neill (1957) provides five examples of subspecies of amphibians and reptiles that occur in the same region, but remain ecologically segregated in north Florida. At the very least, Neill's study provides many testable hypotheses that could be addressed with molecular studies to explain modern biogeographic distributions that may have resulted from climatic and sea-level changes in the past.

Robertson and Kushlan (1974) discuss the historical biogeography of birds in south Florida, defined as that area of the peninsula "south of the Caloosahatchee and St. Lucie outlets of Lake Okeechobee" (p. 414), and the depauperate condition of avian communities in this region. These communities are dominated by continental taxa that winter in or migrate to Florida (61% of 296 species); breeding birds account for only 116 species (39%). Although the diversity of wading birds remains relatively high, the land birds in south Florida show lower diversity and density compared to other areas with similar habitat in the southeastern USA. Robertson and Kushlan (1974) argue that the impoverished state for these land birds is the result of withdrawal of continental birds to the north after the last full glacial, in which sea levels lowered by as much as 60–80 m or more (Blackwelder et al. 1979; Bloom 1983; Fairbanks 1989). Such a drastic lowering of sea level probably transformed south Florida into a broad region of largely upland continental habitat and faunas. The Everglades probably did not develop as a unique habitat until relatively recently, after sea level began to rise to its current position (Blackwelder et al. 1979; Bloom 1983).

This model of avian community development in south Florida contrasts with classic models of biogeography that attribute impoverished faunas in peninsulas to a peninsular effect, whereby these regions are similar to islands in having limited access for colonization by continental species (Simpson 1964). Robertson and Kushlan (1974) reject this argument and point out that during the Wisconsinan glaciation, the coastal plain of south Florida was two to three times larger than today and would have been quite accessible for invasion by continental forms. Instead, these authors suggest that loss of habitat through climatic change and sea-level rise would have caused withdrawal of continental birds to the north, and colonization of West Indian species from the south, resulting in the impoverished diversity of breeding land birds in south Florida today. The lack of habitat heterogeneity in this region also probably restricts its biological diversity (Means and Simberloff 1987). Support for this model by Robertson and Kushlan (1974) is found in the fossil data presented below.

SYSTEMATIC PALEONTOLOGY

The systematic ordering and taxonomy of fossil birds presented below follow those of the American Ornithologists' Union (AOU 1983) and its subsequent supplements through the 41st (AOU 1997) except for the use of Vulturidae (= Cathartidae) in the Ciconiiformes (see Ligon 1967; Rea 1983), and the recognition of the monophyletic order Accipitriformes instead of the polyphyletic Falconiformes (Ligon 1967; Jollie 1976–1977; Rea 1983; Emslie 1988a; but see Griffiths 1994 for an alternative view). All measurements given below are in mm.

Class AVES
Order GAVIIFORMES
Family GAVIIDAE

Gavia pacifica (Lawrence 1858)

Referred material.—Inglis 1A: left ulna missing distal end, UF 30050.

Measurements.—UF 30050 measures proximal breadth and depth, 12.7 and 12.6 (range, 10.6–11.6 and 10.7–12.0, respectively, in *G. pacifica,* $n = 3$ males), and least breadth and depth of shaft, 7.0 and 5.7 (range, 6.6–7.1, 5.1–5.5 in *G. pacifica*), respectively.

Description.—This specimen is intermediate in size between *Gavia stellata,* the smallest living loon, and *G. immer.* It compares well in size and characters to *G. pacifica* except that the fossil is slightly more robust.

This specimen also was compared to four ulnae of the extinct species *Gavia concinna* from the Pliocene Bone Valley Formation, Florida (Brodkorb 1963b). UF 30050 differs from this species by the tubercle for attachment of the anterior ligament, which is short and broad in *G. concinna* as described by Wetmore (1940), but longer and narrower in *G. pacifica* and UF 30050. Two other fossil loons from the North American Pliocene, *G. palaeodytes* and *G. howardae,* are smaller than *G. concinna* (see Emslie 1995a).

Discussion.—This specimen is the first fossil record of *Gavia pacifica* in Florida. The species is a rare and irregular visitor to Florida today, with ca. 20 sightings reported up to 1992 (Stevenson and Anderson 1994).

Gavia immer (Brünnich 1764)

Referred material.—Cutler Hammock: humeral end left coracoid, UF 102205. Pelican Road Shell Pit: left carpometacarpus missing proximal end, UF 159592.

Discussion.—This species is a common winter resident on the Gulf Coast of north Florida and is rare in south Florida (Stevenson and Anderson 1994). The two fossil records suggest that *Gavia immer* may have been more common in south Florida during the Pleistocene. The species also has been reported from the late Pleistocene of Rock Springs, Florida (Woolfenden 1959) and Bell Cave, Alabama (Parmalee 1992).

Gavia concinna Wetmore 1940

Referred material.—Forsberg Shell Pit: distal right tarsometatarsus, UF 159446.

Description.—The specimen is recognized as *Gavia concinna* by its small distal foramen and the posterior border of the middle trochlea, which extends farther proximad than in the living species *G. stellata, G. pacifica, G. adamsii,* and *G. immer.* It compares well with UF 82968, a distal left tarsometatarsus from Leisey Shell Pit 1A referred to *G. concinna* by Emslie (1995a).

Discussion.—This small, extinct loon also is known from the early Pliocene (late Hemphillian, 5.2–4.5 Ma) Bone Valley Formation, Florida (Wetmore 1940; Brodkorb 1963b). UF 159446 is only the second Irvingtonian record for this species.

Order PODICIPEDIFORMES

Family PODICIPEDIDAE

Tachybaptus dominicus (Linnaeus 1766)

Referred material.—Inglis 1A: left ulna, UF 30129.

Measurements.—The specimen measures length, 45.4; proximal breadth and depth, 4.1 and 3.5; least breadth and depth of shaft, 1.8 and 2.0; distal breadth and depth, 3.0 and 2.9.

Description.—The specimen compares most closely in size to females of the living *Tachybaptus dominicus,* and differs in having a larger attachment for anterior articular ligament and broader external cotyla ($n = 6$, USNM). The fossil specimen also was compared to *Rollandia rolland* ($n = 2$ females, USNM), which has an ulna with a more prominent internal condyle, less distinct impression of M. brachialis anticus, and border to external cotyla flaring more palmad than in UF 30129.

One fossil species of grebe, *Pliolymbus baryosteus* from the late Pliocene of Kansas, is small and robust (Murray 1967). A nearly complete ulna (UMMP 27173) of this species is longer and more robust (length, 53.7; least breadth and depth of shaft, 2.7 and 3.2; Murray 1967) than UF 30129.

Discussion.—This specimen is only the second fossil record for *Tachybaptus dominicus* in North America; Steadman (1984) reported one bone of this species from the early Pleistocene (late early Irvingtonian) locality at Payne Creek, Florida. The Least Grebe is a rare and irregular visitor to Florida today and only six sightings have been reported (Stevenson and Anderson 1994). It is resident from southern Texas and Mexico south to Peru and Argentina, and in the Greater Antilles (Stevenson and Anderson 1994).

Podilymbus podiceps (Linnaeus 1758)

Referred material.—Cutler Hammock: sternal half right coracoid, UF 159253; two proximal right humeri, UF 101540, 159159; proximal left humerus, UF

159156; three distal right humeri, UF 101543, 159161, 159256; two distal left humeri, UF 159162, 159255; proximal left ulna, UF 101542; proximal left carpometacarpus, UF 159273; proximal left femur, UF 159254; three distal right femora, UF 159155, 159160, 159264; four distal right tibiotarsi, UF 101544, 159157, 159158, 159257; left tarsometatarsus missing distal external and middle trochlea, UF 159258; two proximal left tarsometatarsi, UF 101541, 159260; two distal right tarsometatarsi, UF 159163, 159259; distal left tarsometatarsus, UF 159154.

Lecanto 2A: left tarsometatarsus, UF 101535; sternum, UF 128748.

McLeod Limerock Mine, Pocket A: right tibiotarsus, AMNH 27770.

D&M Shell Pit: proximal left humerus, UF 159461; distal right tibiotarsus, UF 159463; distal left tibiotarsus, UF 159462.

Forsberg Shell Pit: right tarsometatarsus, UF 129095.

Pelican Road Shell Pit: sternal half right coracoid, UF 159598; two distal left humeri, UF 159599, 159600.

Haile 7C: proximal right humerus, UF 159395; proximal left tarsometatarsus, UF 159396.

Inglis 1A: left humerus, UF 30133; proximal left ulna, UF 30135; distal left ulna, UF 30134; proximal right tibiotarsus, UF 30138; two distal right tibiotarsi, UF 30136, 30137.

Description.—These specimens compare well in size and characters to the living species.

Discussion.—The Pied-billed Grebe is one of the more common species in the fossil record in Florida. It also is one of the oldest of all living avian species with a geologic range that extends to the early Pliocene (late Hemphillian; 5.2–4.5 Ma; Becker 1987a). Well-preserved fossils from Macasphalt Shell Pit, Sarasota County, Florida, indicate that this species had a slightly smaller and more delicate bill in the late Pliocene than it does today (Emslie 1992).

Storer (1976, 1992) reviewed the fossil record and geographic variation in skeletal measurements of *Podilymbus* in North America. He concluded that two fossil species are valid: *P. majusculus* from the late Pliocene of Idaho, and *P. wetmorei* from the late Pleistocene of Florida. The former species is distinguished by its longer and more slender tarsometatarsus and shorter, more robust femur, whereas the latter has a shorter tarsometatarsus and more robust femur, compared to *P. podiceps*. The validity of *P. wetmorei* has been questioned by Steadman (1984). None of the fossils reported here has the characteristics of these extinct species.

Podiceps sp.

Referred material.—Inglis 1A: right humerus missing proximal end, UF 30130; distal left ulna, UF 30132.

Measurements.—UF 30130 measures distal breadth and depth, 7.5 and 6.0; least breadth and depth shaft, 3.9 and 3.6, respectively. UF 30132 measures distal breadth and depth, 5.2 and 4.8; least breadth and depth shaft, 3.5 and 2.9, respectively.

Description.—These specimens are slightly larger and more robust than those of the male Horned Grebe (*Podiceps auritus*). Comparable mean measurements of *P. auritus* (n = 11 males, FLMNH and USNM) are, humerus distal breadth and depth, 7.5 ± 0.3 (range, 7.0–8.1) and 5.2 ± 0.2 (5.0–5.5); least breadth and depth of shaft, 3.7 ± 0.1 (3.5–3.8) and 3.6 ± 0.2 (3.2–4.0); ulna distal breadth and depth, 4.8 ± 0.1 (4.7–5.0) and 4.3 ± 0.1 (4.1–4.5); least breadth and depth of shaft, 2.6 ± 0.1 (2.5–2.7) and 3.3 ± 0.1 (3.1–3.4).

Discussion.—Fossil species of *Podiceps* are reviewed by Murray (1967) and Emslie (1995a). Brodkorb (1963b) described the fossil species *Podiceps dixi* from a proximal carpometacarpus from the late Pleistocene of Florida. It was recognized by its distinctly larger size compared to *P. auritus,* and smaller size compared to *P. grisegena* and *P. nigricollis,* and may represent a large, Pleistocene form of *P. auritus* (Steadman 1984). The material from Inglis 1A indicates that this large form existed throughout the Pleistocene.

Podicipedidae, indeterminate

Referred material.—Cutler Hammock: distal left tibiotarsus, UF 159209.
Inglis 1A: carina of sternum, UF 30131.

Description.—These specimens are too fragmentary for generic identification.

Order PELECANIFORMES
Family PHALACROCORACIDAE

Phalacrocorax cf. *P. auritus* (Lesson 1831)

Referred material.—Forsberg Shell Pit: proximal left femur, UF 129093; distal right tibiotarsus, UF 129094.

Discussion.—*Phalacrocorax auritus* has been reported from numerous late Pleistocene and Holocene (archaeological) sites in Florida (Brodkorb 1963b), but is rare from early Pleistocene sites. Fossils referred to *Phalacrocorax* sp. and similar in size to male *P. auritus* or *P. penicillatus* were reported from Leisey Shell Pit 1A, 3 and 3B (Emslie 1995a).

Phalacrocorax idahensis (Marsh 1870)

Referred material.—Inglis 1C: three cervical vertebrae, UF 165536, 165562, 165583; left ulna, UF 165532; distal right ulna, UF 165567; left carpometacarpus, UF 165530 (Fig. 4); right carpometacarpus, UF 165544; right tarsometatarsus, UF 165531 (Fig. 4).

Measurements.—UF 165532 measures length, 166.2; proximal breadth and depth, 11.4 and 11.3; least breadth and depth of shaft, 6.4 and 5.9; distal breadth and depth, 10.5 and 9.1. Similar measurements for UF 165530 are: 79.0, 6.8 and 14.6, 5.1 and 3.6, 7.2 and 8.2, respectively. The tarsometatarsus (UF 165531) measures length, 72.2; proximal breadth and depth, 15.0 and 19.6; least breadth and depth of shaft, 6.2 and 4.7; distal breadth, 16.6; breadth and depth of middle trochlea, 5.8 and 7.9.

Description.—The ulnae (UF 165532 and 165567) and carpometacarpi (UF 165530 and 165544) appear to be from the same individuals based on their close similarity in size and features. These last two specimens and UF 165531 compare well with a referred carpometacarpus (UMMP 55564) and tarsometatarsus (UMMP 49571) of *Phalacrocorax idahensis* from Hagerman, Glenns Ferry Formation, Idaho. In particular, the carpometacarpus (UMMP 55564) has a blunt metacarpal I, giving it a squarish shape, and is very similar to the type carpo-

FIG. 4. Left carpometacarpus (left, UF 165530) and right tarsometatarsus (right, UF 165531) of *Phalacrocorax idahensis* from Inglis 1C, Florida. Scale 1×; bar = 1 cm.

metacarpus of *P. idahensis* at the Yale Peabody Museum (YPM 527; see Murray 1970). Moreover, UF 165530 and 165544 have an internal rim to the carpal trochlea less rounded than in *P. auritus,* a feature considered distinctive for *P. idahensis* by Murray (1970). Additional characters that separate *P. idahensis* from other living and fossil cormorants are provided by Murray (1970) and Emslie (1995b). All specimens reported here fall within the size and features of those described for *P. idahensis.*

Discussion.—These specimens are the first true record of *Phalacrocorax idahensis* from Florida. A specimen referred to this species by Brodkorb (1955) from the early Pliocene Bone Valley Formation, Florida, probably represents another large, extinct species (Brodkorb 1963b). Other records of *P. idahensis* are restricted to the late Pliocene of the western USA. The species is best known from numerous complete and partial elements from Hagerman, Idaho (Glenns Ferry Formation, Blancan III of Repenning 1987, 3.7–3.2 Ma; Murray 1970); Castle Creek, Idaho (the type locality; Marsh 1870), and Rexroad 3, Kansas (Blancan II of Repenning 1987, 4.25–3.7 Ma; Murray 1970). The specimens from Inglis 1C are the youngest for this species and extend its geologic range into the latest Pliocene. The presence of this species in the latest Pliocene of Florida adds to a growing list of avian taxa that occurred in the western and eastern USA, indicating dispersal of species between these regions (see Discussion below).

Family ANHINGIDAE

Anhinga anhinga (Linnaeus 1766)

Referred material.—Cutler Hammock: distal right tibiotarsus, UF 159082.

D&M Shell Pit: proximal right humerus, UF 159448; distal right humerus, UF 159449.

FIG. 5. Anterior (left) and posterior (right) views of the holotypical right tibiotarsus (UF 95948) of *Anhinga beckeri*, new species, from Leisey Shell Pit 1A, Florida. Scale 1×; bar = 1 cm.

Anhinga beckeri, new species
(Fig. 5)

Holotype.—Right tibiotarsus, UF 95948.

Type locality and age.—Leisey Shell Pit 3A, Sec. 15, T32S, R18E (Ruskin Quadrangle, USGS 7.5-minute series), Hillsborough County, Florida; early Pleistocene (late–early Irvingtonian), 1.5–1.0 Ma (Morgan and Hulbert 1995).

Paratypes.—Cutler Hammock: distal left humerus, UF 102203; distal left tibiotarsus, UF 102204.

Coleman 3C: distal left ulna, UF 16664.

D&M Shell Pit: distal left humerus, UF 159432; distal right ulna, UF 159451; distal left ulna, UF 159452; distal right tibiotarsus, UF 159431.

Measurements.—See Tables 4 and 5.

Diagnosis.—Tibiotarsus short and robust (longer with more slender shaft in *Anhinga anhinga, A. rufa,* and *A. melanogaster*; Table 5), enlarged and prominent ligamental attachment on proximal internal shaft (attachment smaller and weakly developed in *A. anhinga, A. rufa,* and *A. melanogaster*), shaft external to inner cnemial crest broadly excavated (excavation shallow and not as broad in *A. anhinga, A. rufa,* and *A. melanogaster*; Fig. 5).

Description.—Humerus with anterior articular ligament short (attachment is longer and angled more proximad in *A. anhinga*), ectepicondylar prominence small (prominence larger and more robust in *A. anhinga*). Ulna with longer distal external condyle that extends farther proximad on shaft than in *A. anhinga.* All elements larger and/or more robust than those of *A. anhinga, A. rufa,* and *A. melanogaster* (Tables 4, 5).

TABLE 4. Measurements (mm) of humeri and ulnae of modern and fossil *Anhinga anhinga* and fossil *A. beckeri,* new species, from Florida.*

Species/element	PB	PD	LBS	LDS	DB	DD
Humerus						
Anhinga anhinga						
Mean ± SD (*n* = 13; 6♂, 6♀, 1?)	18.3 ± 0.6	6.7 ± 0.3	6.5 ± 0.3	5.5 ± 0.3	13.4 ± 0.5	10.0 ± 0.3
Range	17.5–19.6	6.2–7.0	6.0–6.9	4.7–5.9	12.3–14.0	9.4–10.5
UF 159448	19.6	7.0	—	—	—	—
UF 159449	—	—	6.6	6.2	14.1	8.8
Anhinga beckeri						
UF 159432	—	—	8.7	6.7	16.1	10.0
UF 102203	—	—	8.0	6.7	16.0	11.9
Ulna						
Anhinga anhinga						
Mean ± SD (*n* = 10; 5♂, 5♀)			5.9 ± 0.2	5.0 ± 0.2	9.1 ± 0.3	8.7 ± 0.4
Range			5.6–6.2	4.8–5.2	8.2–9.4	8.0–9.3
Anhinga beckeri						
UF 16664			6.4	5.5	9.9	9.1
UF 159461			6.7	5.5	9.1	9.5
UF 159452			6.6	5.6	10.2	9.2

* PB = proximal breadth; PD = proximal depth; LBS = least breadth shaft; LDS = least depth shaft; DB = distal breadth; DD = distal depth.

Etymology.—Named for Jonathan J. Becker in recognition of his contributions on the fossil record of birds in Florida.

Discussion.—Only two fossil species of *Anhinga* have been described from North America. Becker (1986a, 1987b) discussed and reviewed these taxa, *A. subvolans* (formerly *Phalacrocorax subvolans*) and *A. grandis,* and referred a partial skeleton from the late Miocene of Florida to this latter species. He also was first to point out that another large, indeterminate anhinga was present in the late Pleistocene of Florida, known only from a distal ulna (UF 16664) from Coleman 3C that Ritchie (1980) had referred to *Anhinga* cf. *A. grandis.* The additional specimens reported here and in Emslie (1995a) verify the existence of this large species in Florida. The co-occurrence of *A. beckeri* and the living species *A. anhinga* at Cutler Hammock and D&M Shell Pit provides evidence that these species coexisted throughout the Pleistocene in south Florida.

Anhingas represent a tropical to subtropical group of birds that has been present in Florida and South America since the early Miocene (Becker 1986a; Rasmussen and Kay 1992; Campbell 1996). Two extinct genera and three species have been described from South America: *Meganhinga chilensis* from the early Miocene of Chile (Alvarenga 1995), *Macranhinga paranensis* from the late Miocene of Argentina, and *Anhinga fraileyi* from the late Miocene of Peru (Campbell 1996). Campbell (1996) questioned the validity of *Meganhinga* and *Macranhinga* as genera distinct from *Anhinga.* In addition, based on measurements in Campbell (1996, tables 2–4), the humerus of *A. beckeri* is approximately the same size as that of *A. fraileyi,* but the tibiotarsus for the latter species is much longer and larger than in *A. beckeri.* Material of *Meganhinga chilensis* and *Macranhinga paranensis* was not available for comparison, but the age and location of these

TABLE 5. Measurements (mm) of tibiotarsi of *Anhinga* sp. and fossils of *Anhinga beckeri*, new species, from Florida.*

Species	L	PB	PD	LBS	LDS	DB	DD
Anhinga anhinga							
(*n* = 13; 6♂, 6♀, 1?)							
Mean ± SD	84.5 ± 2.4	10.2 ± 0.3	15.4 ± 0.7	5.2 ± 0.3	4.2 ± 0.1	10.3 ± 0.4	9.1 ± 0.3
Range	79.4–88.3	9.5–10.9	14.3–17.1	4.6–5.7	4.0–4.4	9.6–10.8	8.5–9.8
Anhinga rufa							
(*n* = 2♀)	88.2–89.2	11.2–11.7	16.3–17.7	5.5	4.6	10.2–10.9	10.2–10.6
Anhinga melanogaster							
(*n* = 1?)	87.7	9.9	15.0	5.1	4.0	10.0	9.4
Anhinga beckeri							
UF 95948	82.7	11.0	15.6	6.3	5.3	10.6	10.0
UF 102204	—	—	—	—	—	12.2	—
UF 159431	—	—	—	6.4	4.6	10.6	10.3

* L = length; PB = proximal breadth; PD = proximal depth; LBS = least breadth shaft; LDS = least depth shaft; DB = distal breadth; DD = distal depth.

fossils make it unlikely that *A. beckeri* is synonymous with either of these taxa. Only one species, *A. anhinga,* occurs in the New World today, and it is largely tropical in distribution (Johnsgard 1993). It is a common year-round resident through most of Florida, where it inhabits freshwater to brackish lakes, ponds, and rivers (Stevenson and Anderson 1994).

Order CICONIIFORMES
Family ARDEIDAE

Botaurus lentiginosus (Rackett 1813)

Referred material.—Inglis 1A: left carpometacarpus missing metacarpal III, UF 30125.

Discussion.—This specimen compares well in size and characters to females of *Botaurus lentiginosus.* Only one extinct bittern is known from North America, *Botaurus hibbardi* from the late Pliocene of Kansas (Moseley and Feduccia 1975). This taxon, however, is known only by a distal femur and is not comparable with the specimen from Inglis 1A; it also is distinctly smaller than *B. lentiginosus.* Two coracoids of a small bittern from the late Pliocene Macasphalt Shell Pit were referred to this genus by Emslie (1992) and may represent *B. hibbardi* based on their relative size. Specimens of *B. lentiginosus* also were recovered from this site (Emslie 1992) and indicate coexistence of at least two species of *Botaurus* in the late Pliocene in Florida. *Botaurus lentiginosus* also has been reported from the late Pleistocene localities of Seminole Field, Rock Springs, and Vero Beach, Florida (Brodkorb 1963b).

Ixobrychus exilis (Gmelin 1789)

Referred material.—Lecanto 2A: distal right tarsometatarsus, UF 101538.

Inglis 1A: distal left tibiotarsus, UF 30126; distal left tarsometatarsus, UF 30127.

Discussion.—*Ixobrychus exilis* also has been reported from Macasphalt Shell Pit (Emslie 1992). The specimens from Inglis 1A were presumed to represent an undescribed species by Carr (1981). However, the supposed differences between the fossil specimens and *Ixobrychus exilis* described by Carr (1981) are within the range of variation observed in a large series of skeletons of the latter species.

Ardea herodias Linneaus 1758

Referred material.—Cutler Hammock: proximal left humerus, UF 159079.

Shell Materials Pit: right femur, UF 91011.

Description.—UF 159079 and UF 91011 compare well in size and characters to *Ardea herodias.*

Ardea sp.

Referred material.—Inglis 1A: carina of sternum, UF 30124.

Description.—UF 30124 has the apex of the carina positioned higher above the manubrium than in *Ardea herodias.* A humeral coracoid from Macasphalt Shell Pit may represent an extinct species of *Ardea* from the late Pliocene of Florida (Emslie 1992) and it is possible that UF 30124 also represents this taxon.

Butorides virescens (Linnaeus 1758)

Referred material.—Cutler Hammock: distal left tarsometatarsus, UF 159203.

De Soto Shell Pit 5: distal right tarsometatarsus, UF 159436.

Discussion.—Campbell (1976) described the fossil species *Butorides validipes* from the late Pliocene locality of Haile 15A, Florida. The specimens listed here do not possess those characters of the tarsometatarsus used by Campbell (1976) to distinguish that extinct taxon, and they compare more closely to those of *B. virescens.*

Family THRESKIORNITHIDAE

Eudocimus albus (Linnaeus 1758) or *E. ruber* (Linnaeus 1758)

Referred material.—Cutler Hammock: proximal right scapula, UF 159377.

Inglis 1A: proximal left humerus, UF 30128.

Description.—Bones of these two species overlap in size and characters. The fragmentary specimens here cannot be distinguished to either taxon.

Eudocimus leiseyi Emslie 1995

Referred material.—D&M Shell Pit: shaft left tarsometatarsus, UF 159450.

Forsberg Shell Pit: distal right tibiotarsus, UF 129096.

Description.—UF 159450 and UF 129096 are distinguished as *Eudocimus* by their small size, presence of divergent borders of the anterior metatarsal groove, and deep posterior intercondylar fossa (borders parallel and intercondylar fossa shallower in *Plegadis*; Emslie 1995a). The specimens compare well in size and characters to those of *E. leiseyi* (Emslie 1995a).

Discussion.—This extinct ibis is known from two other localities in Florida, the late Pliocene Macasphalt Shell Pit and early Pleistocene Leisey Shell Pit (the type locality; Emslie 1992, 1995a). Its presence at two additional early Pleistocene sites listed above suggests that it was common in south Florida during that period.

Family CICONIIDAE

Ciconia maltha L. Miller 1910

Referred material.—Cutler Hammock: midsection of right coracoid, UF 159080; distal right tarsometatarsus missing middle and internal trochleae, UF 159094.

McLeod Limerock Mine, Pocket A: distal left tarsometatarsus, AMNH 27787.

D&M Shell Pit: humeral half left coracoid, UF 159447.

De Soto Shell Pit 5: distal left tarsometatarsus, UF 159433.

Forsberg Shell Pit: right carpometacarpus missing proximal end and metacarpal III, UF 159444; distal left femur, UF 159441; distal left tibiotarsus, UF 159440.

Pelican Road Shell Pit: two distal right tibiotarsi, UF 156786, 156787; distal left tibiotarsus, UF 156785.

Discussion.—This large, extinct stork commonly occurs in the fossil record of Florida. Two undescribed species in this genus also are known from the early Pliocene Bone Valley Formation and the late Miocene–early Pliocene Big Sandy Formation, Arizona (Becker 1987a; Bickart 1990). However, large variation in size between sexes in modern *Ciconia* make it difficult to determine whether or not two or more species occurred in the Plio–Pleistocene (see also Howard 1942).

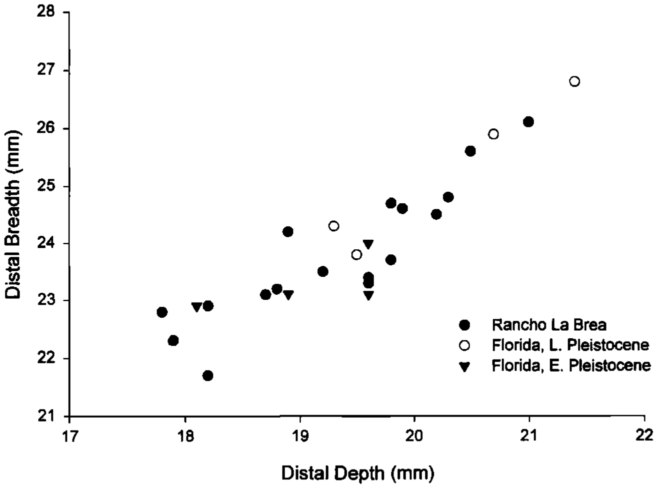

FIG. 6. Scatter plot of measurements of the distal breadth and depth of fossil tarsometatarsi referred to *Ciconia maltha* from Florida and Rancho La Brea, California; symbols indicate relative age of each specimen. Note the large variation in size in specimens from Rancho La Brea and the tendency for increased body size from early to late Pleistocene in specimens from Florida.

Specimens referred to *Ciconia maltha* from the late Pleistocene of Rancho La Brea, California, show considerable variation in body size, as shown by measurements of the distal tibiotarsus (Fig. 6). Specimens from the early and late Pleistocene of Florida, however, indicate a tendency for an increase in body size through time with only slight overlap in size between early and late Pleistocene material (Fig. 6). A humeral left coracoid (UF 123869; depth at glenoid fossa, 17.9; least breadth shaft, 9.5) from a small *Ciconia* at Leisey Shell Pit 3 (Emslie 1995a) is much smaller than UF 159080 (least breadth shaft, 12.5) and 159447 (depth at glenoid fossa, 20.5; least breadth shaft, 10.5) and may represent an undescribed species.

Family TERATORNITHIDAE

Teratornis merriami L. Miller 1909

Referred material.—Cutler Hammock: midsection of left coracoid, UF 159138; proximal left radius, UF 102238; distal left radius, UF 159116; proximal right tarsometatarsus, UF 102237; pedal phalanx, UF 102239.

Reddick 1A: distal left carpometacarpus, UF 95650.

Discussion.—*Teratornis merriami* is well known from the late Pleistocene of Florida and western North America. UF 95650 from Reddick 1A is the first record of this species from this locality. A partial skeleton referred to this species from the early Pleistocene locality, Leisey Shell Pit 1A (Emslie 1995a), may represent an undescribed species (K. Campbell, pers. comm.). A second species of teratorn, *T. incredibilis,* is much larger than *T. merriami* and a fragmentary specimen was tentatively referred to this species from the early Pleistocene locality at Leisey Shell Pit 3 (Emslie 1995a).

Family VULTURIDAE

Coragyps atratus (Bechstein 1793)

Referred material.—Cutler Hammock: two right quadrates, UF 159110, 159207; humeral right coracoid, UF 159143; humeral left coracoid, UF 159142; proximal right scapula, UF 159076; proximal left scapula, UF 159087; distal right humerus, UF 159125; shaft left humerus, UF 159085; shaft right ulna, UF 159088; two proximal right radii, UF 102241, 102245; proximal left radius, UF 159136; distal left radius, UF 159140; proximal left carpometacarpus, UF 102242; proximal right tibiotarsus, UF 102247; two distal right tibiotarsi, UF 102240, 102244; four distal left tibiotarsi, UF 102243, 159081, 159141, 159144; left fibula, UF 102250; proximal right tarsometatarsus, UF 159124; shaft right tarsometatarsus, UF 159194; two proximal left tarsometatarsi, UF 102248, 159137 (juvenile); shaft left tarsometatarsus, UF 159057; two distal right tarsometatarsi, UF 102246, 159135; distal left tarsometatarsus, UF 159193.

Haile 16A: two proximal left mandibles, UF 31949, 31950; proximal right mandible, UF 31948; right coracoid missing portions of both ends, UF 31952; proximal right humerus, UF 31951; proximal left ulna, UF 31955; proximal left ulna (juvenile), UF 31954; distal right ulna (juvenile), UF 159488; distal right radius, UF 159489; two proximal right carpometacarpi, UF 159484, 159485; digit II phalanx I, UF 31915; proximal left femur, UF 31956; distal left femur, UF 159486; distal right tibiotarsus, UF 31953; distal right tarsometatarsus, UF 31958; two distal left tarsometatarsi, UF 31957, 159487 (juvenile).

McLeod Limerock Mine, Pocket A: two right coracoids, AMNH 27778, 27780; distal left humerus, AMNH 27781; distal right humerus, AMNH 27782; distal left tibiotarsus, AMNH 27793; three distal right tibiotarsi, AMNH 27779, 27791, 27792.

Inglis 1A: left quadrate, UF 30107; axis vertebra (juvenile), UF 30100; proximal left scapula, UF 30101; humeral left coracoid (juvenile), UF 30097; two right coracoids (both juvenile), UF 30096, 30098; right humerus missing proximal end (juvenile), UF 30087; distal left humerus (juvenile), UF 30088; proximal right ulna, UF 30089; two proximal left ulnae, UF 30090, 30091; two distal left ulnae, UF 30092, 30093 (juvenile); right ulnare (juvenile), UF 30103; right radiale (juvenile), UF 30102; proximal left carpometacarpus, UF 30099; distal right tibiotarsus, UF 30095; right tarsometatarsus missing distal end (juvenile), UF 30094; proximal left tarsometatarsus (juvenile), UF 30108.

Discussion.—*Coragyps atratus* also has been reported from numerous other late Pleistocene and Holocene sites in Florida (Brodkorb 1964). The rich fossil record for the Black Vulture implies that it has been common in Florida since the late Pliocene, whereas *Cathartes aura* has not been reported earlier than the late Pleistocene. Both species are common in Florida today (Stevenson and Anderson 1994).

Cathartes aura (Linnaeus 1758)

Referred material.—Cutler Hammock: distal left humerus, UF 159150; left ulnare, UF 102249.

Lecanto 2A: distal left tibiotarsus (juvenile), UF 101531; left tarsometatarsus (juvenile), UF 101532.

Discussion.—This species also has been reported from numerous other late Pleistocene and Holocene sites in Florida and western North America (Brodkorb 1964). Its absence in fossil sites older than the late Pleistocene suggests that it is a relatively recent arrival in North America.

Gymnogyps californianus (Shaw 1798)

Referred material.—Cutler Hammock: partial right quadrate, UF 159123; left quadrate, UF 159192; distal left humerus, UF 159128; shaft right ulna, UF 102210; proximal right carpometacarpus, UF 159121; pollex, UF 102214; cervical vertebrae, UF 102211; distal right femur, UF 105795; proximal right tibiotarsus, UF 102213; distal right tarsometatarsus missing external trochlea, UF 159118; distal right tarsometatarsus missing external and internal trochleae, UF 159130; two external trochleae of right tarsometatarsi, UF 102215, 159191; internal trochlea of left tarsometatarsus, UF 159164; distal pedal phalanx, UF 102212.

Discussion.—*Gymnogyps californianus* has been reported from numerous late Pleistocene sites in western North America, Florida (Emslie 1987a, b), and New York (Steadman and Miller 1987).

Gymnogyps kofordi Emslie 1988

Referred material.—Haile 16A: see Emslie (1988a).

Peace River Mine: proximal left carpometacarpus, UF 28889.

Description.—UF 28889 compares well in size and characters to a complete right carpometacarpus (UF 31918) of *Gymnogyps kofordi* from Haile 16A. The Peace River Mine locality (early Pliocene, 5.2–4.5 Ma, Bone Valley Formation) includes an early Pleistocene (Irvingtonian) component, equivalent in age to Haile 16A, with which UF 28889 is assumed to be affiliated.

cf. *Gymnogyps* sp.

Referred material.—Inglis 1A: proximal left tibiotarsus, UF 30068.

Description.—This specimen, too worn and fragmentary for positive identification, is similar to *Gymnogyps* in size and morphology, but may represent another genus (see below). One other specimen, a pedal phalanx from Macaphalt Shell Pit, also was tentatively referred to this genus by Emslie (1992).

Aizenogyps, new genus

Type species.—*Aizenogyps toomeyae,* new species.

Diagnosis.—Tarsometatarsus recognized as Vulturidae by deep anterior metatarsal groove, large intercondylar process, and shape and relative position of the trochleae; humerus with deep, elongated brachial impression, large ectepicondylar and entepicondylar prominences, and deep and broad ligamental furrow (Rea 1983). Tarsometatarsus differs from *Plesiocathartes, Diatropornis, Gymnogyps, Breagyps, Vultur, Geronogyps, Sarcoramphus, Pliogyps, Coragyps,* and *Cathartes* by shaft more robust (see measurements below); shaft straight with little flaring at proximal and distal ends as in *Hadrogyps* (shaft distinctly flared in *Vultur, Sarcoramphus, Geronogyps, Pliogyps, Brasilogyps, Cathartes,* and *Coragyps*); anterior metatarsal groove deeper proximally and extends more than half the length of the shaft as in *Sarcoramphus* (groove shallower in *Gymnogyps,* extends only to half the length of the shaft in *Gymnogyps, Vultur, Geronogyps, Breagyps,* *Cathartes,* and *Coragyps*); proximal and distal foramina small (foramina distinctly larger in *Hadrogyps,* moderately large in *Pliogyps*); external surface of intercotylar prominence with deep notch (notch shallow to absent in *Gymnogyps, Vultur, Sarcoramphus, Cathartes,* and *Coragyps*); intercotylar depression in proximal view large, round, and deeply excavated (depression small and shallow in *Gymnogyps, Vultur, Sarcoramphus, Cathartes,* and *Coragyps*); in posterior view, hypotarsus forms broad plate that is nearly as deep (proximo-distally) as it is wide (similar in *Coragyps*; plate is distinctly broader than it is deep in *Gymnogyps, Vultur, Geronogyps, Pliogyps,* and *Sarcoramphus*); proximal external border of hypotarsus without notch as in *Cathartes* (deep to shallow notch present in *Vultur* and *Geronogyps,* notch shallow to absent in *Gymnogyps* and *Coragyps*); presence of deep excavation on posterior proximal shaft, internal to ridge below hypotarsus (shaft shallowly to moderately excavated in *Gymnogyps, Vultur, Sarcoramphus, Cathartes,* and *Coragyps*); ridges on posterior borders of internal and external shaft high and distinct (ridges low and less distinct in *Gymnogyps, Sarcoramphus, Cathartes,* and *Coragyps*); metatarsal facet oriented nearer internal side of shaft as in *Vultur* and *Cathartes* (facet positioned more posterior in *Gymnogyps, Sarcoramphus,* and *Coragyps*); shaft above external trochlea depressed and angled externally to point level with proximal border of metatarsal facet (little or no depressed area in *Gymnogyps, Vultur, Geronogyps, Sarcoramphus, Cathartes,* and *Coragyps*); middle trochlea short proximo-distally as in *Gymnogyps* (longer in *Vultur* and *Hadrogyps*).

Humerus with deltoid crest broad and flared as in *Geronogyps, Cathartes,* and *Coragyps,* extending farther distally before joining shaft (crest is smaller, less flared, and joins shaft more proximally in *Gymnogyps, Vultur,* and *Sarcoramphus*); pneumatic foramen shallow with broad, rounded proximal border as in *Cathartes* (foramen deep in *Gymnogyps, Vultur,* and *Coragyps,* shallow to deep in *Sarcoramphus,* and with narrow proximal border in *Gymnogyps*); groove between head and internal tuberosity deep (groove shallow in *Gymnogyps,* shallow to moderately deep in *Vultur* and *Sarcoramphus,* groove pneumatic to partially pneumatic in *Coragyps* and *Cathartes*); internal border of deltoid crest large and prominent and distinctly raised above level of shaft (crest remains flush or only slightly raised above shaft in *Geronogyps, Gymnogyps, Vultur, Sarcoramphus, Cathartes,* and *Coragyps*); deltoid crest ends distally with large, oblong tubercle (tubercle is smaller and more rounded in *Gymnogyps, Vultur, Cathartes,* and *Coragyps*); impression of M. brachialis anticus without pneumatism (impression pneumatic in *Coragyps* and longer proximo-distally in *Cathartes*); attachment for anterior articular ligament broad as in *Vultur* (attachment is narrower in *Gymnogyps* and *Cathartes*). Measurements of modern and fossil condor humeri are provided in Table 6.

Description.—Size large and tarsometatarsus broader and more robust than all other fossil and living genera of New World vultures. The stout, columnar shaft of the tarsometatarsus is shared with only one other genus, *Hadrogyps,* from the middle Miocene of California (Emslie 1988b). *Hadrogyps* is smaller than *Aizenogyps* and is near the size of the King Vulture (*Sarcoramphus papa*), and it differs from *Aizenogyps* and all other vulture genera by its large proximal and distal foramina on the tarsometatarsus, among other characters (Emslie 1988b).

TABLE 6. Measurements (mm) of humeri of modern and fossil condors and fossils of *Aizenogyps toomeyae*, new genus and species, from Florida.*

Species	L	PB	PD	LBS	LDS	DB	DD
Gymnogyps californianus (*n* = 26; 4♂, 1♀, 21?)							
Mean ± SD	266.5 ± 6.6	54.9 ± 1.6	18.1 ± 1.6	20.2 ± 1.0	16.5 ± 1.0	49.1 ± 1.5	26.4 ± 1.0
Range	256.5–277.0	50.7–57.0	15.3–19.2	17.8–22.0	14.8–18.3	44.7–51.8	23.2–28.1
Vultur gryphus (*n* = 14; 1♂, 1♀, 21?)							
Mean ± SD	274.9 ± 9.6	60.7 ± 2.2	18.5 ± 0.9	21.0 ± 0.9	17.2 ± 1.0	52.3 ± 1.6	27.4 ± 0.9
Range	258.0–292.0	56.7–63.8	17.5–20.2	18.9–22.5	15.8–19.1	49.9–55.1	25.5–30.0
Dryornis pampeanus							
MLP 169.-20	—	—	—	29.8	18.1	54.9	28.2
Aizenogyps toomeyae							
UF 149290	275	60.8	19.4	22.6	17.5	52.4	26.8

* L = length; PB = proximal breadth; PD = proximal depth; LBS = least breadth shaft; LDS = least depth shaft; DB = distal breadth; DD = distal depth.

Etymology.—From Greek *aizenos,* for powerful and vigorous, and *gyps,* masculine, vulture.

Discussion.—Other extinct genera and species of Vulturidae include *Brasilogyps faustoi* from the Deseadan of Brazil, *Dryornis pampeanus* from the Montehermosan of Argentina, *Pliogyps fisheri* from the Pliocene of Kansas, *P. charon* from the Miocene of Florida, *Geronogyps reliquus* from the late Pleistocene of Peru (Campbell 1979), and *Breagyps clarki* from the late Pleistocene of western North America. Of these, *Brasilogyps* is a small vulture that closely resembles *Coragyps atratus* in size and features (Alvarenga 1985), and *Dryornis pampeanus* is a large condor near the size of *Aizenogyps* that was closely related to *Vultur* (Tonni 1980). *Dryornis* is known by a distal humerus and femur. The distal humerus differs from that of *Aizenogyps* by its slightly greater size (Table 6) and by a larger and more robust ectepicondylar process that extends farther proximad on the shaft (based on illustration in Moreno and Mercerat 1891). *Pliogyps fisheri* and *P. charon* were medium-sized vultures with short legs and heavy bodies (Tordoff 1959; Becker 1986b). *Geronogyps* and *Breagyps* also were closely related to *Vultur* (Emslie 1988b) and differ from *Aizenogyps* and other vulture genera in characters listed above and by Miller (1910), Campbell (1979), and Emslie (1988b).

A possible new genus of condor from the middle Pliocene of Argentina (C. Tambussi, pers. comm.) is represented by a worn proximal ulna and radius, neither of which can be compared to *Aizenogyps.* The fossil record, however, indicates a high diversity of condors (three genera and four species) in this region of South America during the Pliocene (C. Tambussi, pers. comm.). Two extinct genera and species, *Plesiocathartes europaeus* and *Diatropornis ellioti,* in the family Vulturidae also are known from the late Eocene–early Oligocene of France. These were small vultures, with tarsometatarsi 25–50% smaller than that of *Cathartes aura* (Cracraft and Rich 1972), and differ from *Aizenogyps* by characters given above. All other fossil genera referred to Vulturidae, but no longer considered valid, are reviewed by Emslie (1988a).

Aizenogyps toomeyae, new species
(Fig. 7)

Holotype.—Left tarsometatarsus, UF 159428.

Type locality and age.—Haile 7C, Alachua County, Florida; latest Pliocene (latest Blancan; ca. 2.0 Ma; Morgan and Hulbert 1995).

Paratypes.—Fifteenth cervical vertebra, UF 159430; third thoracic vertebra, UF 159429; left humerus (shaft restored; Fig. 8), UF 149290.

Measurements.—UF 159428 measures length, 127.9; proximal breadth and depth, 29.2 and 22.5; least breadth and depth of shaft, 17.0 and 9.2; distal breadth, 32.8; breadth and depth of internal trochlea, 9.3 and 14.8; middle trochlea, 12.4 and 17.0; and external trochlea, 7.8 and 15.2. Comparative measurements of other fossil and modern condor tarsometatarsi are provided in Emslie (1988a, b).

Diagnosis.—As for the genus.

Etymology.—Named for Barbara Toomey, who discovered some of the type material, in recognition of her contributions to vertebrate paleontology in Florida.

Discussion.—All elements represent a minimum of one adult individual, but were not found in association. This large condor represents the third extinct genus

FIG. 7. Anterior (left) and posterior (right) views of the holotypical left tarsometatarsus (UF 159428) of *Aizenogyps toomeyae*, new genus and species, from Haile 7C, Florida. Scale 1×; bar = 1 cm.

(along with *Pliogyps* and *Breagyps*) to be described from the Plio–Pleistocene of North America. It also is the third species (along with *Gymnogyps californianus* and *G. kofordi*) of condor to be recorded from the Plio–Pleistocene of Florida, which indicates the former diversity of this group in this region.

The presence of *Aizenogyps toomeyae* in deposits at Haile 7C that are roughly equivalent in age to those at Macasphalt Shell Pit and Inglis 1A, from where fragmentary fossils were referred to *Gymnogyps* sp., raises the possibility that these latter specimens actually represent *Aizenogyps*. The proximal tibiotarsus (UF 30068) from Inglis 1A is similar in size and characters to *Gymnogyps californianus* and was tentatively referred to that species by Carr (1981). Emslie (1988a) determined that this specimen lacked sufficient characters for specific identification and referred it to *Gymnogyps* sp. The specimen also differs from *Gymnogyps* by the shape of the inner cnemial crest, which flares upward and is distinctly

FIG. 8. Anconal (left) and palmar (right) views of the paratype left humerus (UF 149290) of *Aizenogyps toomeyae*, new genus and species, from Haile 7C, Florida. Scale 0.5×; bar = 5 cm.

higher above the interarticular surface in *G. californianus* and *Vultur gryphus* (in UF 30068, the crest does not flare and extends to the level of the interarticular surface, similar to *Sarcoramphus papa, Cathartes aura,* and *Coragyps atratus*). Given these differences, it is possible that UF 30068 represents *A. toomeyae.* A pedal phalanx (UF 113400) referred to cf. *Gymnogyps* sp. by Emslie (1992) from Macasphalt Shell Pit is similar to *G. kofordi* in size and characters. However, phalanges do not always provide reliable characters for distinguishing genera and this specimen could represent *Aizenogyps* rather than *Gymnogyps.* Thus, it is not possible now to determine whether or not two condors may have coexisted in the late Pliocene of Florida.

Order ANSERIFORMES
Family ANATIDAE

Anabernicula gracilenta Ross 1935

Referred material.—Inglis 1A: right quadrate, UF 30140; left tarsometatarsus missing hypotarsus and internal trochlea, UF 30141.

Measurements.—UF 30141 measures length, 61.6; breadth and depth of middle trochlea, 4.9 and 7.1.

Discussion.—*Anabernicula gracilenta* also is known from Macasphalt Shell Pit and Leisey Shell Pit 1A (Emslie 1992, 1995a). A distal tarsometatarsus (UF 113366) from Macasphalt compares well with UF 30141 except for the slightly smaller size of the former (least breadth and depth of shaft, 3.9 and 3.1; breadth and depth of middle trochlea, 4.4 and 6.7). One other species, *Anabernicula minuscula,* is known from the late Pliocene Richardson Road Shell Pit, Florida (Emslie 1995b). Two other species of *Anabernicula* are known from late Pliocene through late Pleistocene sites of North America. The genus has been reported tentatively from the late Miocene–early Pliocene of Arizona (Bickart 1990).

Pigmy geese are closely related to shelducks (tribe Tadornini; Howard 1964a), a group that is widespread in Asia and Europe, but neither group occurs in North America today. The earliest record of this group in the New World is from the middle Miocene Calvert Formation, Maryland (Alvarez and Olson 1978). Pigmy geese reached their greatest diversity in North America during the Pleistocene.

Aix sponsa (Linnaeus 1758)

Referred material.—Haile 7C: associated left ulna, radius, and carpometacarpus, UF 121744.

De Soto Shell Pit 5: humeral half right coracoid, UF 159437.

Inglis 1A: proximal right scapula, UF 30155; humeral right coracoid, UF 30157; furculum, UF 30156; right humerus, UF 30153; right ulna missing proximal end, UF 30149; distal left carpometacarpus, UF 30154.

Discussion.—These specimens represent the earliest fossil record of *Aix sponsa* in North America. The species also is known from several late Pleistocene sites in Florida (Brodkorb 1964).

Anas crecca Linnaeus 1758

Referred material.—Lecanto 2A: left carpometacarpus, UF 101536.

D&M Shell Pit: left coracoid missing sternal end, UF 159456.

De Soto Shell Pit 5: right humerus, UF 159435.

Anas crecca Linnaeus 1758 or *A. discors* Linnaeus 1766

Referred material.—De Soto Shell Pit 5: proximal half left humerus, UF 159438.

Inglis 1A: left humerus, UF 30144; shaft left humerus, UF 30145; left ulna, UF 30148; right carpometacarpus, UF 30146; left carpometacarpus, UF 30147.

Anas platyrhynchos Linneaus 1758

Referred material.—Cutler Hammock: proximal left scapula, UF 101548; two proximal right ulnae, UF 101546, 102202; distal left ulna, UF 101547; right femur missing distal end, UF 159205.

Inglis 1A: proximal left humerus, UF 30142; partial sternum, UF 30143.

Anas discors Linnaeus 1766 or *A. cyanoptera* Vieillot 1816

Referred material.—Haile 7C: left coracoid, UF 159409.

Anas clypeata Linnaeus 1758

Referred material.—Haile 7C: right coracoid, UF 159410; proximal right humerus, UF 159417.

D&M Shell Pit: right coracoid missing head, UF 159453.

Anas sp.

Referred material.—Cutler Hammock: proximal left carpometacarpus, UF 159355.

Pelican Road Shell Pit: proximal right ulna, UF 156781; proximal left radius, UF 156782.

Haile 7C: right coracoid with ends damaged, UF 159415; distal left ulna, UF 159413; distal right radius, UF 159418.

Inglis 1A: shaft right humerus, UF 30152; proximal left ulna, UF 30150; partial left femur, UF 30151.

Description.—UF 30150 and 30151 are from a duck near the size of *Anas clypeata* or *A. strepera*; UF 30152 is near *A. acuta* in size.

Aythya sp.

Referred material.—D&M Shell Pit: right carpometacarpus, UF 159458.

Forsberg Shell Pit: left coracoid, UF 159445.

Inglis 1A: left ulna, UF 30139.

Bucephala albeola (Linnaeus 1758)

Referred material.—Haile 7C: right tarsometatarsus, UF 159412.

D&M Shell Pit: left coracoid with ends damaged, UF 159457.

Lophodytes cucullatus (Linnaeus 1758)

Referred material.—Shell Materials Pit: right humerus, UF 91012.

Mergus sp.

Referred material.—Cutler Hammock: proximal left tibiotarsus, UF 102201.

Haile 7C: anterior carina of sternum, UF 159412.

Oxyura jamaicensis (Gmelin 1789)

Referred material.—Cutler Hammock: humeral right coracoid, UF 101549; proximal left ulna, UF 159284.

Anatidae, indeterminate

Referred material.—Cutler Hammock: left scapula, UF 159269; midsection of right coracoid, UF 101550; humeral end right coracoid, UF 101550.

Haile 7C: four associated cervical vertebrae, UF 121745; right coracoid with humeral end damaged, UF 159414; left humerus with ends damaged, UF 159411; associated right humerus, radius, and ulna (cemented in matrix), UF 159419.

Order ACCIPITRIFORMES
Family ACCIPITRIDAE

Pandion haliaetus (Linnaeus 1758)

Referred material.—Cutler Hammock: proximal right humerus, UF 159095; distal right tibiotarsus, UF 159152.

Discussion.—Remains of osprey are uncommon in the fossil record, but have been reported from two other late Pleistocene sites in Florida, the Ichetucknee River (Campbell 1980) and Rock Springs (Woolfenden 1959). Only two fossil species are known, *Pandion homalopteron* from the middle Miocene of California (Warter 1976) and *P. lovensis* from the late Miocene of Florida (Becker 1985b).

Haliaeetus leucocephalus (Linnaeus 1766)

Referred material.—Cutler Hammock: proximal right scapula, UF 159169; proximal right carpometacarpus, UF 102217; pedal phalanx missing distal end, UF 159167.

Neophrontops slaughteri Feduccia 1974

Referred material.—Inglis 1A: left mandible, UF 30081; left coracoid missing head, UF 30080; distal right ulna, UF 30083; shaft right radius, UF 30086; proximal left radius, UF 30085; distal left radius, UF 30084; right femur, UF 30082 (Fig. 9); proximal half left tibiotarsus, UF 30078; distal half right tibiotarsus, UF 30079 (Fig. 9); proximal half right tarsometatarsus, UF 30076; distal half right tarsometatarsus, UF 30077 (Fig. 9).

Measurements.—The femur (UF 30082) measures length, 94.3; proximal breadth, 20.8; least breadth and depth of shaft, 9.7 and 9.7; distal breadth and depth, 23.6 and 17.9. The distal tibiotarsus (UF 30079) measures least breadth and depth of shaft, 7.5 and 6.4; distal breadth and depth, 15.6 and 11.7. The distal tarsometatarsus (UF 30077) measures least breadth and depth of shaft, 6.7 and 5.0; distal breadth, 17.3; breadth and depth of middle trochlea, 5.8 and 7.8.

Description.—These specimens are recognized as *Neophrontops* by characters of the tibiotarsus and tarsometatarsus as described by Miller (1916) and Howard (1932). UF 30079 was found to be identical in size and characters to the type distal tibiotarsus (UMMP 52265) of *N. slaughteri* from the late Pliocene Hagerman local fauna, Idaho (Feduccia 1974). Specifically, UF 30079 has a deep intercondylar fossa, broad tendinal groove, and pronounced ligamental prominence similar to *N. slaughteri*; these characters also distinguish this species from *N. americana* (Feduccia 1974).

Five other fossil species of *Neophrontops* have been described, three of which are much smaller than *N. slaughteri.* These three species, *N. vetustus* from the late Hemingfordian of Nebraska, *N. dakotensis* from the early Clarendonian of South Dakota (Compton 1935), and *N. ricardoensis* from the late Clarendonian of California (Rich 1980), also are much older in age than *N. slaughteri.* Two other species, *N. vallecitoensis* from the Irvingtonian of California (Howard 1963) and *N. americanus* from the late Pleistocene of California (Miller 1916) and Wyoming (Emslie 1985), approach the size of *N. slaughteri.* Of these, *N. vallecitoensis* is known only by two distal tarsometatarsi that are distinctly larger than that of *N. americanus* and near the size of UF 30077. The type (LACM 2866) of

FIG. 9. Right femur (left, UF 30082), distal right tibiotarsus (middle, UF 30079), and distal right tarsometatarsus (right, UF 30077) of *Neophrontops slaughteri* from Inglis 1A, Florida. Scale 1×; bar = 1 cm.

N. vallecitoensis was compared to UF 30077 and found to be slightly larger with a metatarsal facet positioned higher on the shaft and middle trochlea deeper than the latter specimen. These differences are shared with *N. americanus,* which also has a longer and narrower metatarsal facet than UF 30077. In addition, the proximal mandible (UF 30081) has a larger and deeper ramus and longer articular processes, the femur (UF 30082) is larger and has a deeper fibular groove, and the tibiotarsus (UF 30078, 30079) is larger with a larger and more robust internal ligamental prominence than in *N. americanus* (mean ± SD of distal breadth and depth, 14.0 ± 0.6 and 11.1 ± 0.5; $n = 10$). Other differences between *N. americanus* and *N. slaughteri* are given by Feduccia (1974).

Discussion.—These specimens represent only the second record and are the most complete fossils now known for *Neophrontops slaughteri.* They also represent the first "Old World" vulture to be reported from the eastern USA. In addition to the six species of *Neophrontops,* Old World vultures also are represented by two other genera and four species in North America, *Palaeoborus rosatus, P. howardae,* and *P. umbrosus* from the Miocene of South Dakota, Nebraska, and New Mexico, respectively (Brodkorb 1964; Becker 1987a), and *Neogyps errans* from the late Pleistocene of western North America (Brodkorb 1964). In addition, Bickart (1990) referred an associated partial skeleton from the late Miocene–early Pliocene of Arizona to *Neophrontops* sp., noting its similarity to *N. americanus* in size, and to *Neophron* in characters. All of these taxa demonstrate the former diversity and wide distribution of Old World vultures in North America prior to their extinction here at the end of the Pleistocene.

Circus cf. *C. cyaneus* (Linnaeus 1766)

Referred material.—Haile 16A: proximal left femur, UF 102365.

Description.—This specimen compares well in characters to modern specimens of *Circus cyaneus* except for its slightly smaller size; it compared most closely in size to one modern specimen (USNM 347847).

Discussion.—Although a common wintering species in Florida today (Stevenson and Anderson 1994), this specimen is the first fossil record for *Circus cyaneus* in the state. It also is known from numerous late Pleistocene and Holocene sites in the western USA (Brodkorb 1964).

Accipiter cooperii (Bonaparte 1828)

Referred material.—Cutler Hammock: proximal right humerus, UF 102219; proximal left tarsometatarsus, UF 159112; distal right tarsometatarsus, UF 159211; distal left tarsometatarsus, UF 159212.

Lecanto 2A: right quadrate, UF 101537.

Haile 16A: proximal right tibiotarsus, UF 31936.

Inglis 1A: right ulna, UF 30075; distal right ulna, UF 30074; distal left ulna, UF 30073; proximal right tibiotarsus, UF 30071; proximal left tibiotarsus, UF 30072; distal right tibiotarsus, UF 30070.

Buteogallus urubitinga (Gmelin 1788)

Referred material.—Inglis 1A: left tarsometatarsus missing distal end, UF 30069 (Fig. 10).

Measurements.—The specimen measures proximal breadth, 17.0; least breadth shaft, 7.4.

Description.—This specimen originally was referred to the extinct *Buteogallus fragilis* by Carr (1981), but it compares well within the size and variation of *B. urubitinga* (*n* = 11, USNM, 5♂, 3♀, 2?; mean ± SD of proximal breadth, 15.9 ± 0.9; least breadth shaft, 7.0 ± 0.6). It also was compared to 10 left tarsometatarsi from Rancho La Brea, California, referred to *B. fragilis* (proximal breadth, 17.2 ± 1.0; least breadth shaft, 8.2 ± 0.7). Although UF 30069 is incomplete, it appears to be longer and narrower, with a deeper posterior groove on the shaft, than in *B. fragilis*. One other extinct species, *B. milleri,* also is known from the late Pleistocene of California and is slightly more robust than *B. fragilis* (Howard 1932).

Buteogallus fragilis L. Miller 1911a

Referred material.—Pelican Road Shell Pit: distal left tibiotarsus, UF 156783 (Fig. 10).

Measurements.—The specimen measures least breadth and depth of shaft, 10.7 and 6.4; distal breadth and depth, 18.2 and 12.2.

Description.—The specimen compares well in characters to eight left tibiotarsi of *Buteogallus fragilis* from Rancho La Brea (mean ± SD distal breadth and depth, 16.7 ± 1.1 and 11.4 ± 0.6), but is slightly larger in size. It also was compared to a series of 11 tibiotarsi of *B. urubitinga* (USNM, 5♂, 3♀, 2?; least

FIG. 10. Left tarsometatarsus missing distal end (UF 30069) of *Buteogallus urubitinga* from Inglis 1A (left), and distal left tibiotarsus (UF 156783) of *B. fragilis* from Pelican Road Shell Pit, Florida. Scale 1×; bar = 1 cm.

breadth and depth of shaft, 8.5 ± 0.5 and 5.4 ± 0.2; distal breadth and depth, 15.1 ± 0.8 and 10.3 ± 0.5). UF 156783 is larger with a more robust shaft and broader intercondylar fossa in anterior view than in *B. urubitinga.*

Discussion.—This specimen, and that of *Buteogallus urubitinga* above, represent the earliest records of these hawks from North America and the first to be reported from the eastern USA. The extinct *B. fragilis* is well known from the late Pleistocene tar pits at Rancho La Brea, Carpenteria, and McKittrick, California, and also has been reported from Shelter Cave, New Mexico (Howard and Miller 1933). It appears to have been closely related to the living *B. urubitinga* and possibly shared tropical origins with that species. Both of these hawks add to a growing list of fossil birds from Florida with tropical and western North American affinities that began appearing in the peninsula in the late Pliocene.

Buteo lineatus (Gmelin 1788)

Referred material.—Cutler Hammock: proximal right scapula, UF 159379; right coracoid, UF 159083; humeral right coracoid, UF 159277; proximal left humerus, UF 159129; distal left humerus, UF 102251; proximal right ulna, UF 159267; right carpometacarpus, UF 159072; proximal left femur, UF 159217; proximal right tibiotarsus, UF 102252; distal right tibiotarsus, UF 159216; proximal left tarsometatarsus, UF 159114; distal right tarsometatarsus, UF 159210.

Lecanto 2A: premaxilla, UF 128755; distal left radius, UF 101494; right femur, UF 101495; 2 distal left tarsometatarsi, UF 101496, 101497; ungual phalanx, UF 101498.

Haile 16A: humeral half of left coracoid, UF 31935.

De Soto Shell Pit 5: proximal left scapula, UF 159434.

Buteo cf. *B. jamaicensis* (Gmelin 1788)

Referred material.—Cutler Hammock: proximal left ulna, UF 102234; three distal left ulnae, UF 102236, 159074, 159166; proximal right tarsometatarsus, UF 159131; proximal left tarsometatarsus, UF 159126; pedal phalanx, UF 159165.

Buteo swainsoni Bonaparte 1838 or *B. lagopus* (Pontoppidan 1763)

Referred material.—Cutler Hammock: distal left tibiotarsus, UF 159132.

Buteo sp.

Referred material.—Cutler Hammock: sternal half left coracoid, UF 159077; proximal right femur, UF 159188; proximal right tarsometatarsus, UF 159219; proximal left tarsometatarsus, UF 159117; distal right tarsometatarsus missing external trochlea, UF 159374; two ungual phalanges, UF 102235, 159218.

Lecanto 2A: pedal phalanx, UF 128756.

Haile 16A: right coracoid missing portion of humeral end, UF 31937.

McLeod Limerock Mine, Pocket A: distal right tibiotarsus, AMNH 27771.

Inglis 1A: proximal left ulna, UF 30052; left carpometacarpus, UF 30051; proximal left carpometacarpus, UF 30064; wing phalanx, UF 30067; two left acetabulae, UF 30065, 30066; synsacrum, UF 30054; distal left tibiotarsus, UF 30053; two proximal left tarsometatarsi, UF 30056, 30057; distal left tarsometatarsus, UF 30055; pedal phalanx, UF 30058; five ungual phalanges, UF 30059, 30060–30063.

Description.—These specimens are within the range of variation of characters for various living species of *Buteo* and cannot be reliably identified to species. The specimens from Haile 16A and Inglis 1A are from a large hawk, slightly larger and more robust than *Buteo jamaicensis* and *B. regalis.* They may represent an extinct taxon, or a large temporal form of a living species.

cf. *Buteo* sp.

Referred material.—Inglis 1C: shaft of right coracoid, UF 165624.

Description.—The specimen is near the size and features of *Buteo lineatus,* but is too fragmentary for positive identification even to genus.

Amplibuteo woodwardi (L. Miller 1911a)

Referred material.—McLeod Limerock Mine, Pocket A: distal left ulna, AMNH 27783; distal right ulna, AMNH 27784; two proximal right carpometacarpi, AMNH 27772, 27773; distal left carpometacarpus, AMNH 27774; proximal left femur, AMNH 27794; distal left femur, AMNH 27775; right femur missing proximal end, AMNH 27795; distal half of left tarsometatarsus, AMNH 27788; distal right tarsometatarsus, AMNH 27789.

Ichetucknee River: proximal half of right femur (pathological), AMNH 28005.

Description.—These specimens compare well in size and characters to those of *Amplibuteo woodwardi,* an extinct eagle known from one other late Pleistocene site in Florida, the Aucilla River (Emslie 1995a). AMNH 27772–27774, 27788, and 27789 also were compared to the carpometacarpi and tarsometatarus of a partial, associated skeleton (UF 102550) referred to *Amplibuteo* sp. from Leisey Shell Pit 3B (Emslie 1995a). All elements of this skeleton except the carpometacarpus are similar to those of *A. woodwardi* and the specimens from McLeod Limerock Mine. The carpometacarpus also differs from an undescribed species of *Amplibuteo* by characters given by Emslie and Czaplewski (in press). Thus, the Leisey specimen appears to represent an undescribed species that existed in the early Pleistocene in Florida.

Campbell (1980) described *Amplibuteo hibbardi* from the late Pleistocene of Peru. The distal tarsometatarsi from Florida (AMNH 27788 and 27789) were compared to a cast (ROM 16905) of the holotype of *A. hibbardi* at LACM and differ from this species in characters given by Emslie (1995a).

Amplibuteo sp. Emslie and Czaplewski, in press

Referred material.—Haile 7C: humeral left coracoid, UF 159404; left furculum, UF 159403; carina of sternum, UF 159402; right and left humeri (matching) with shafts broken, UF 159406, 159407; right and left ulnae (matching), UF 121743, 159405; distal left radius, UF 159408; right carpometacarpus, UF 159426; partial synsacrum, UF 159427.

Inglis 1C: associated right coracoid and fragmentary manubrium of sternum, UF 165529; left humerus missing distal end, UF 165542; left fibula, UF 165577.

Discussion.—This material is described elsewhere with additional material from the late Pliocene of Arizona (Emslie and Czaplewski, in press). It represents the oldest record for, and only the third species to be described in, this extinct genus.

Aquila chrysaetos (Linnaeus 1758)

Referred material.—Cutler Hammock: right distal tarsometatarsus missing external trochlea, UF 159127; pedal phalanx, UF 159151; two ungual phalanges, UF 159133, 159215.

Discussion.—The only other record of *Aquila chrysaetos* from Florida is a distal femur (UF 22095) from the middle Pleistocene Coleman 2A (Ritchie 1980). The Golden Eagle rarely occurs in Florida today (Stevenson and Anderson 1994).

Aquila sp. Emslie and Czaplewski, in press

Referred material.—Inglis 1A: fragment of left cranium, UF 159544; proximal left mandible, UF 30028; two distal mandibles, UF 30029, 30030; two proximal left scapulae, UF 30026, 30027; shaft left coracoid, UF 30034; anterior carina of sternum, UF 30035; distal right humerus with end damaged, UF 30043; two proximal left humeri, UF 30040, 30041; two proximal left ulnae, UF 30023, 30024; distal left ulna, UF 30025; two proximal right radii, UF 30038, 30039; proximal left radius, UF 30037; distal left radius, UF 30036; right carpometacarpus, UF 30015; distal left carpometacarpus, UF 30014; three wing phalanges, UF 30031–30033; two proximal right femora, UF 30020, 30021; distal right femur, UF 30022; left femur, UF 30019; right tibiotarsus, UF 30012; proximal right fibula, UF 30013; right metatarsal I, UF 30018; right subterminal phalanx of digit I, UF 30016; left ungual phalanx of digit II, UF 30017; right phalanx II of digit II, UF 30045; left phalanx I of digit III, UF 30046; phalanx III of digit III, UF

30044; right phalanx I of digit IV, UF 30047; ungual phalanx of digit IV, UF 30048.

Discussion.—This large, long-legged eagle is being described elsewhere with additional specimens from the late Pliocene of Arizona (Emslie and Czaplewski, in press).

Spizaetus grinnelli (L. Miller 1911a)

Referred material.—Cutler Hammock: two proximal right carpometacarpi, UF 102218, 159153.

Description.—These specimens are recognized by the metacarpal I, which is more strongly angled proximally in *Spizaetus* and the fossil material than in *Buteo, Accipiter, Aquila, Pandion,* and *Haliaeetus.* Although too fragmentary to measure, the specimens resemble those of *S. grinnelli* from Rancho La Brea, California, in their large size, the most distinguishing feature of this species compared to the living *S. ornatus* and *S. tyrannus* (Howard 1932).

Discussion.—*Spizaetus grinnelli* is known from only one other fossil site in Florida, the late Pleistocene locality at West Palm Beach (Becker 1985a). It is closely related to the living Ornate Hawk-Eagle (*Spizaetus ornatus*) that occurs in tropical forests in Mexico and Central and South America (Brown and Amadon 1968). Three other fossil species have been described, but are not known by carpometacarpi: *Spizaetus pliogryps* from the late Pleistocene of Fossil Lake, Oregon (Shufeldt 1891), *S. willetti* from the late Pleistocene of Smith Creek Cave, Nevada (Howard 1935), and *S. tanneri* from the early Pleistocene of Nebraska (Martin 1971). One other fossil, a distal tibiotarsus referred to *Spizaetus* sp. from Macasphalt Shell Pit, may represent an undescribed species and is the earliest record for the genus (Emslie 1992).

Family FALCONIDAE

Caracara plancus (J. F. Miller 1777)

Referred material.—Cutler Hammock: two proximal left scapulae, UF 102231, 159084; humeral half left coracoid, UF 159078; proximal right humerus, UF 102225; proximal left humerus, UF 102364; distal left humerus, UF 159148; three distal left ulnae, UF 102226, 159067, 159303; distal right radius, UF 102232; proximal left carpometacarpus, UF 102228; two distal left carpometacarpi, UF 102229, 102230; proximal right femur, UF 102227; proximal left femur, UF 159119; proximal right tibiotarsus, UF 102223; two distal right tibiotarsi, UF 159146, 159196; three distal left tibiotarsi, UF 102224, 159122, 159145; three proximal right tarsometatarsi, UF 102221, 102222, 159149; three proximal left tarsometatarsi, UF 159120, 159147, 159195; two distal right tarsometatarsi, UF 159115, 159251; ungual phalanx, UF 159197.

Description.—This material compares well in size and characters to the living species.

Discussion.—Fossils of the Crested Caracara have been reported from only one other locality in Florida, at Haile 11B (late Pleistocene; Ligon 1965). At least three individuals are represented at Cutler Hammock. The presence of this species implies that grasslands, the preferred habitat for this species in Florida today, were located near the site in the late Pleistocene (Stevenson and Anderson 1994).

TABLE 7. Measurements (mm) of tibiotarsi of *Milvago chimango* and *M. chimachima* and fossil material from Florida.*

Species	L	LBS	LDS	DB	DD
Milvago chimango (*n* = 9; 2♂, 7?)					
Mean ± SD	70.5 ± 3.1	4.1 ± 0.4	3.2 ± 0.3	7.8 ± 0.7	6.4 ± 0.4
Range	67.0–77.4	3.7–5.0	2.7–3.6	7.1–9.5	6.0–7.3
Milvago chimachima (*n* = 8; 1♂, 2♀, 5?)					
Mean ± SD	70.1 ± 1.4	4.2 ± 0.2	3.1 ± 0.2	8.3 ± 0.4	6.7 ± 0.4
Range	67.7–72.9	3.9–4.4	2.9–3.4	7.5–8.9	6.2–7.2
Fossils					
UF 22562	—	4.8	3.6	8.8	7.3
UF 95900	—	5.1	3.4	8.4	7.1
UF 102233	—	4.5	3.1	—	—

* L = length; LBS = least breadth shaft; LDS = least depth shaft; DB = distal breadth; DD = distal depth.

The absence of caracara remains in sites older than the late Pleistocene suggests that this species did not arrive in Florida until that time.

Milvago chimachima Bangs and Penard 1918

Referred material.—Cutler Hammock: humeral left coracoid, UF 159278; proximal left carpometacarpus, UF 159356; distal right femur, UF 159221; distal left tibiotarsus, UF 102233; proximal left tarsometatarsus, UF 159220.

Reddick 1A: distal left tibiotarsus, UF 95900.

Arredondo 2A: distal left tibiotarsus, UF/PB 1692.

Ichetucknee River: right tibiotarsus missing proximal end, UF 22562; distal left tarsometatarsus, UF 22561.

Measurements.—See Tables 7 and 8.

Description.—The fossil species *Falco readei* was described from a distal tibiotarsus from the late Pleistocene deposits at Arredondo 2A, Florida (Brodkorb 1959). Later, Campbell (1980) restudied the holotype and two other specimens (UF 22561, 22562 listed above) from the late Pleistocene Ichetucknee River locality and placed all material within the genus *Milvago.* Until now, these three fossils, representing only two skeletal elements, were the only records of this extinct caracara. The new material reported here permits a reevaluation of *M. readei.*

Campbell (1980) presented a description of characters that distinguish the tibiotarsus and tarsometarsus of *Milvago readei* from the living species, *M. chimachima* and *M. chimango.* Comparison of the fossil material with skeletons of these modern species at USNM and FLMNH indicates that the fossils are very similar to *M. chimachima* in size and characters (Tables 7, 8), but differ from *M. chimango* by features noted by Campbell (1980). Using seven skeletons of *M. chimachima* and eight of *M. chimango* seven characters of the tibiotarsus identified by Campbell (1980) to distinguish *M. readei* were found here to be within the range of variation in *M. chimachima.* Specifically, the tibiotarsus of *M. chimachima* exhibits considerable variation in size and robustness of skeletal elements (Table 7), the distal tendinal openings vary in size and position on the shaft, concavities on the external surface of the external condyle and on the posterior-

TABLE 8. Measurements (mm) of tarsometatarsi of *Milvago chimango* and *M. chimachima* and a fossil from Florida.*

Species	L	PB	PD	LBS	LDS	DB	MTB	MTD
Milvago chimango (*n* = 9; 2♂, 7?)								
Mean ± SD	59.7 ± 2.1	8.5 ± 0.8	7.7 ± 0.6	3.2 ± 0.3	2.4 ± 0.2	8.8 ± 0.6	3.2 ± 0.2	3.7 ± 0.3
Range	56.8–63.8	7.9–10.1	7.1–9.0	2.9–3.8	2.2–2.7	8.2–10.2	3.0–3.7	3.4–4.2
Milvago chimachima (*n* = 8; 1♂, 2♀, 5?)								
Mean ± SD	51.8 ± 1.5	8.8 ± 0.3	7.7 ± 0.2	3.5 ± 0.2	2.5 ± 0.1	8.7 ± 0.6	3.3 ± 0.2	4.1 ± 0.3
Range	50.0–54.2	8.5–9.5	7.4–8.0	3.2–3.7	2.3–2.7	8.2–10.0	3.2–3.8	3.7–4.5
Fossil								
UF 22561	—	—	—	3.8	2.6	8.8	3.4	4.3

* L = length; PB = proximal breadth; PD = proximal depth; LBS = least breadth shaft; LDS = least depth shaft; DB = distal breadth; MTB = middle trochlea breadth; MTD = middle trochlea depth.

internal surface of the internal condyle vary from moderately deep to deep (Campbell's characters 1, 2), a deep pit on the external side of the anterior intercondylar fossa and the intercondylar groove in anterior view varies from shallow to deep (characters 3, 4), a tendinal fossa deeply undercuts the external condyle in one modern specimen and varies considerably in shape (character 5), the supratendinal bridge is highly variable in size and in the angle that it extends from distal to proximal ends so that the proximal end is near to far from the external edge of the shaft (character 6), and the shaft varies from slender to robust (Table 7).

The tarsometatarsus of *Milvago chimango* is longer, with a more slender shaft, than *M. chimachima* and the fossil material (Table 8). Characters of this element also vary considerably. Of the seven features of this element discussed by Campbell (1980), the wing of the inner trochlea varies in size and in the extent it is projected and rotated posteriad; one specimen of modern *M. chimachima* (USNM 343844) is similar to UF 22561 in these features (characters 1, 2). The internal intertrochlear notch is narrow and deep in the fossil material as noted by Campbell (1980; character 3), but in modern *M. chimachima* the groove on the middle trochlea varies from narrow and deep to broad and shallow (character 4), a distinct groove posterior from internal intertrochlear notch to the metatarsal facet (character 5) is present in UF 22561 and in one modern specimen of *M. chimachima* (USNM 559321), the shaft is robust with a weak to distinct ridge leading proximad from the metatarsal facet (character 6), and the metatarsal facet is small to large, with UF 22561 similar to USNM 343844.

Based on these comparisons, the only feature of the fossil material outside the range of variation observed in modern skeletons of *Milvago chimachima* is the larger size and robustness of the former. Thus, all fossil material is considered here to represent the living species *M. chimachima,* but may be recognizable as a large, temporal paleosubspecies, *M. chimachima readei.* Two fossil species have been described in this genus, *Milvago alexandri* from the late Pleistocene of Haiti (Olson 1976a) and *M. brodkorbi* from the late Pleistocene of Peru (Campbell 1980); both taxa differ from *M. chimachima* in characters given by Olson (1976a) and Campbell (1980).

Discussion.—The fossil material constitutes the first record of the Yellow-headed Caracara in North America. The species currently ranges from southern Costa Rica to northern Argentina, where it prefers savannah and scrub forest habitats (Brown and Amadon 1968).

Falco sparverius Linnaeus 1758

Referred material.—Cutler Hammock: proximal left tarsometatarsus, UF 159214.

Lecanto 2A: right tarsometatarsus, UF 101499; distal right tarsometatarsus, UF 128758.

Inglis 1A: premaxilla, UF 30115; left coracoid missing sternal end, UF 30117; sternal half right coracoid, UF 30118; two proximal left scapulae, UF 30114, 30116; left humerus missing head, UF 30120; two distal left humeri, UF 30121, 30122; proximal half right ulna, UF 30123; shaft right ulna, UF 159545; partial synsacrum, UF 30119; right femur, UF 30113; distal left femur, UF 30112; proximal left tibiotarsus, UF 30110; proximal right tarsometatarsus, UF 30111.

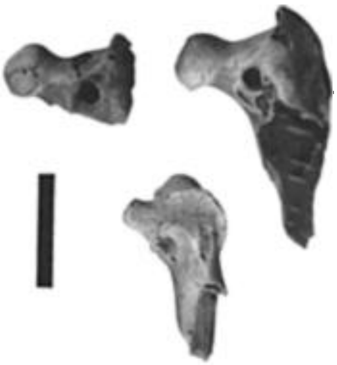

FIG. 11. Proximal right femora (UF 104452, top left; UF 104451, top right) and proximal right carpometacarpus (UF 159490, bottom) of an undetermined genus and species of Cracidae from Haile 16A, Florida. Scale 1.5×; bar = 1 cm.

Falco columbarius Linnaeus 1758

Referred material.—Cutler Hammock: distal right tibiotarsus, UF 102216. Inglis 1A: distal mandible, UF 30104; distal right femur, UF 30105.

Falco cf. *F. peregrinus* Tunstall 1771

Referred material.—Cutler Hammock: distal left ulna, UF 102220.

Discussion.—Fossils of *Falco peregrinus* also have been reported from the late Pleistocene Haile 11B (Ligon 1965) and Arredondo 2A (Brodkorb 1959) localities. This falcon is a regular winter migrant to Florida today, but it does not breed in the state (Stevenson and Anderson 1994).

Order GALLIFORMES

Family CRACIDAE

Cracidae, indeterminate

Referred material.—Haile 16A: proximal left ulna, UF 102400; proximal right carpometacarpus, UF 159490 (Fig. 11); two proximal right femora, UF 104451, 104452 (Fig. 11); distal right femur, UF 104453.

Description.—Recognized as Cracidae, and not Phasianidae, by femur (UF 104451, 104452) lacking pneumatic region on anterior proximal shaft, carpometacarpus (UF 159490) with robust metacarpal I that does not angle proximad and, in proximal view, presence of shelf below carpal trochlea. Among modern cracids, all fossils compare most closely to *Ortalis vetula* in morphology and are slightly larger in size. Specifically, the ulna (UF 102400) has a low olecranon; the morphology of the proximal and distal femur (UF 104451–104453) is similar to that of *O. vetula,* as are muscle scars on the shaft; and the carpometacarpus (UF 159490) has a blunt metacarpal I and pisiform process, with a distinct shelf below the carpal trochlea visible in proximal view. The fossils differ from *O. vetula* in their larger size, ulna with larger impression of M. brachialis anticus with muscle scar on lateral border broader than deep (smaller impression with scar deeper than broad in *O. vetula*), carpometacarpus with metacarpal I more robust (Fig. 11; less robust in *O. vetula*), and femur with lower trochanteric ridge that curves less internally (Fig. 11; ridge higher and curved more internally in *Ortalis*). The femora (UF 104451, 104452) also are distinguished from *Ortalis* and all other Galliformes by the presence of a large foramen on the posterior proximal shaft (Fig. 11).

Discussion.—These specimens probably represent an undescribed genus and species of cracid. If so, it is only the second record of this family in the eastern USA. Brodkorb (1954) described a new genus and species of cracid, ***Boreortalis** laesslei,* from the early Miocene Thomas Farm locality, Florida, based on a distal tibiotarsus (UF/PB 743). Three other fossil cracids (*B. phengites, B. tantala,* and *B. pollicaris*) are each known from one locality, and range in age from the early Miocene to early Pliocene in Nebraska and South Dakota (Wetmore 1923, 1933; Miller 1944). None of these fossil taxa is known by elements comparable to those reported here. The nearest occurrence of a living species of cracid is the Plain Chachalaca (*O. vetula*) with a range extending into southern Texas. Chachalacas prefer brushy clearings in tropical forest, undergrowth along streams, and forest edges (Delacour and Amadon 1973). These habitats are not unlike those indicated by the vertebrate fauna recovered from Haile 16A.

Family PHASIANIDAE

Meleagris gallopavo Linnaeus 1758

Referred material.—Cutler Hammock: cervical vertebra, UF 159134; anterior carina of sternum, UF 102352; shaft left coracoid, UF 102356; humeral left coracoid, UF 159098; shaft right humerus, UF 159053; three proximal left humeri, UF 102353, 159055, 159061; two distal left humeri, UF 102363, 159075; two shafts left ulnae, UF 159062, 159063; distal right ulna, UF 159064; ulnare, UF 159068; right carpometacarpus, UF 102360; distal right carpometacarpus, UF 102355; distal left carpometacarpus, UF 102359; distal digit II phalanx I, UF 102351; proximal wing phalanx, UF 159059; two proximal right femora, UF 102358, 159065; left femur, UF 102361; two proximal left femora, UF 102354, 159092; distal left femur, UF 102357; proximal shaft right tibiotarsus, UF 102299; proximal left tibiotarsus, UF 159054; distal right tibiotarsus, UF 159066; two proximal left tarsometatarsi, UF 102300, 159052; shaft left tarsometatarsus with spur, UF 159060; distal right tarsometatarsus, UF 159056; distal left tarsometatarsus, UF 159051; two pedal phalanges, UF 102362, 159058.

Lecanto 2A: proximal left radius, UF 101480; left tarsometatarsus with spur and missing external and internal trochleae, UF 101479.

Meleagris cf. *M. anza* (Howard 1963) or *M. leopoldi* (A. H. Miller and Bowman 1956)

Referred material.—Haile 7C: paired right and left humeri (juvenile), UF 159425; right femur, UF 159423; right tibiotarsus missing proximal end (juvenile), UF 159422; right tibiotarsus missing distal end, UF 159424; proximal right tarsometatarsus, UF 159420; distal right tarsometatarsus, UF 159421.

Inglis 1A: 1,240 catalogued elements, UF numbers (see Steadman 1980).

Inglis 1C: three cervical vertebrae, UF 165560, 165563, 165581; two sixth thoracic vertebrae, UF 165559, 165564; left ulna, UF 165546; right ulna, UF 165540; right femur, UF 165539; left fibula, UF 165575; right fibula, UF 165578;

left and right tarsometatarsi with spurs, UF 165543, 165554; pedal digit III phalanx III, UF 165557; pedal digit IV phalanx I, UF 165558.

Discussion.—Steadman (1980), in an extensive review of fossil turkeys, found no diagnostic features that could be used to distinguish the two fossil species *Meleagris anza* and *M. leopoldi* and referred all specimens from Inglis 1A to either of these species. The specimens from Haile 7C (UF 159420, 159421) compare well in size and characters to those from Inglis 1A and referral to *M. anza* or *M. leopoldi* is based on these similarities. See Steadman (1980) for a detailed description of each skeletal element of fossil and modern turkeys.

Meleagris sp.

Referred material.—Haile 16A: quadrate, UF 31919; proximal left scapula, UF 22084; proximal right scapula, UF 22083; proximal right humerus, UF 22082; distal right humerus, UF 22081; distal left ulna, UF 102379; distal right ulna, UF 31922; distal left radius, UF 102380; distal right carpometacarpus, UF 31920; digit II phalanx I, UF 102381; distal half left femur, UF 22086; proximal left tibiotarsus, UF 31921; distal left tibiotarsus, UF 22085; proximal left tarsometatarsus, UF 102382; proximal right tarsometatarsus, UF 102383; distal left tarsometatarsus, UF 102384; two pedal phalanges, UF 22087.

McLeod Limerock Mine, Pocket A: right ulna, AMNH 27785; distal left ulna, AMNH 27786; distal right femur, AMNH 27776.

Description.—Material from Haile 16A lacks diagnostic features for specific identification, but is most similar in size to that from Inglis 1A (see Steadman 1980). The specimens from McLeod Limerock Mine also lack sufficient diagnostic characters.

Colinus virginianus (Linnaeus 1758)

Referred material.—Cutler Hammock: right coracoid, UF 159090; two humeral right coracoids, UF 159189, 159190; humeral left coracoid, UF 159091; two distal right humeri, UF 102297, 159270; left humerus, UF 159097; left humerus missing distal end, UF 159096; proximal left tarsometatarsus, UF 159070.

Lecanto 2A: sternum, UF 101511; left humerus, UF 101510; left ulna (juvenile), UF 128761; left femur, UF 101512; distal left femur, UF 128760.

McLeod Limerock Mine, Pocket C: three crania, AMNH 27946–27948; premaxilla, AMNH 27945; six left coracoids, AMNH 27819–27824; six right coracoids, AMNH 27825–27830; two humeral left and one humeral right coracoids, AMNH 27831; four left scapulae (uncatalogued [uncat.]); five right humeri, AMNH 27839–27842, 27844; three distal right humeri, AMNH 27843; seven left humeri, AMNH 27845, 27847–27850, 27852, 27854; two proximal left humeri, AMNH 27846, 27853; three distal left humeri, AMNH 27851; two associated right humeri, radii, and ulnae, AMNH 27838, 27962; eight left ulnae, AMNH 27855–27862; 10 right ulnae, AMNH 27864–27873; left radius, AMNH 27963; associated left carpometacarpus and coracoid (uncat.); two left carpometacarpi, AMNH 27878, 27879; five right carpometacarpi, AMNH 27874–27877, 27965; six sterna, AMNH 27832–27837; 10 partial synsacra, AMNH 27935–27944; five left femora, AMNH 27913, 27916, 27917, 27932, 27919; 11 right femora, AMNH 27920–27929, 27934; three proximal left femora, AMNH 27914, 27918, 27932; proximal right femur, AMNH 27930; left femur missing proximal end, AMNH

27915; distal right femur, AMNH 27931; associated left femur and tibiotarsus, AMNH 27912; four left tibiotarsi, AMNH 27896–27899; three right tibiotarsi, AMNH 27900, 27907, 27909; three proximal left tibiotarsi, AMNH 27901, 27902; three proximal right tibiotarsi, AMNH 27905, 27908, 27966; two distal left tibiotarsi, AMNH 27903, 27904; six distal right tibiotarsi, AMNH 27906, 27910, 27911; paired associated right and left tibiotarsi and tarsometatarsi, AMNH 27888; associated left tarsometatarsus and distal tibiotarsus, AMNH 27887; seven left tarsometatarsi, AMNH 27889–27895; six right tarsometatarsi, AMNH 27880, 27882–27886; two proximal left tarsometatarsi (uncat.); proximal right tarsometatarsus (uncat.); three distal left tarsometatarsi (uncat.); two distal right tarsometatarsi, AMNH 27881; 33 pedal phalanges, AMNH 27951.

Haile 16A: left coracoid, UF 31929; humeral end left coracoid, UF 31930; sternal end left coracoid, UF 102385; two left humeri, UF 31931, 31933; right humerus, UF 31932; distal right ulna, UF 102386; two left carpometacarpi, UF 31926, 31928; distal left carpometacarpus, UF 31927; left femur, UF 102387; two proximal left femora, UF 102388, 102389; two distal left femora, UF 102390, 102391; proximal right femur, UF 102392; distal right tibiotarsus, UF 105825; distal left tibiotarsus, UF 102396; left tarsometatarsus missing distal end, UF 31934; two proximal right tarsometatarsi, UF 102393, 102394; two distal left tarsometatarsi, UF 102395, 105824.

McLeod Limerock Mine, Pocket A: two right coracoids, AMNH 27797, 27804; left coracoid, AMNH 27796; left humerus, AMNH 27799; two distal left humeri, AMNH 27801, 27802; left ulna, AMNH 27800.

Inglis 1A: 1,048 specimens representing all skeletal elements, UF 30351–31396, 165633, 165636.

Inglis 1C: left scapula, UF 165597; left coracoid, UF 165595; right humerus, UF 165523; distal right radius, UF 165596; right carpometacarpus, UF 165533; proximal right femur, UF 165582; proximal right tibiotarsus, UF 165623; left tibiotarsus missing proximal end, UF 165534.

Discussion.—Fossil and modern species of quail are discussed in detail by Holman (1961). In Florida, the extinct species *Colinus suilium* was described on the basis of numerous complete elements from the late Pleistocene Arredondo 2A locality (Brodkorb 1959). Because this fossil species is only slightly larger and more robust than the living species, *C. virginianus,* Holman (1961) considered it to be a large, temporal form of this latter species. Steadman (1984) agreed with this conclusion and considered *C. suilium* synonymous with *C. virginianus,* noting that the larger form in the Pleistocene probably reflected a cooler climate at that time. The extensive material reported here indicates that this species has existed in Florida since the late Pliocene.

Order GRUIFORMES
Family RALLIDAE

Laterallus cf. *L exilis* (Temminck 1831)

Referred material.—Lecanto 2A: right carpometacarpus, UF 101490; left humerus, UF 101491.

Haile 16A: distal right humerus, UF 105800; distal left humerus, UF 105798.

Measurements.—UF 101491 measures length, 25.5; proximal breadth and depth, 5.0 and 1.4; least breadth and depth of shaft, 1.5 and 1.3; distal breadth and depth, 3.2 and 1.7.

Description.—UF 101491 compares well in size and characters to seven humeri (UF 7137 A–G) referred to *Laterallus exilis* by Olson (1974) from the late Pleistocene Haile 11B locality. The carpometacarpus (UF 101490) from Lecanto 2A is referred to this species based on association in the same site as UF 101491. The specimens from Haile 16A also compare well in size with *L. exilis* (see measurements of humeri of living species in Emslie 1992).

Discussion.—The fossil record of *Laterallus* in Florida is reviewed by Olson (1974) and Emslie (1992). Only two fossil species have been described in North America, *L. insignis* from the late Pliocene of Kansas (Feduccia 1968) and *L. guti* from the late Pleistocene of Florida (Brodkorb 1952). Olson (1974) considered *L. guti* as synonymous with the living species *L. exilis* and referred specimens from Reddick and Haile 11B to the latter taxon. Eight elements referred to *Laterallus* sp. from Macasphalt Shell Pit are slightly larger and more robust than *L. jamaicensis* and may represent *L. insignis* (Emslie 1992).

Rallus elegans Audubon 1834 or *R. longirostris* Boddaert 1783

Referred material.—Cutler Hammock: proximal right ulna, UF 159247; distal left ulna, UF 102208; proximal left carpometacarpus, UF 102209.

Lecanto 2A: proximal left scapula, UF 101487.

Inglis 1A: humeral right coracoid, UF 30319; sternal right coracoid, UF 30318; proximal right ulna, UF 30320; left carpometacarpus, UF 30317; carina of sternum, UF 30316; right tarsometatarsus, UF 30310; left tarsometatarsus, UF 30311; proximal left tarsometatarsus, UF 30323; distal right tarsometatarsus, UF 30326; two distal left tarsometatarsi, UF 30324, 30325.

Inglis 1C: manubrium of sternum, UF 165594; right coracoid, UF 165524.

Description.—Skeletal elements of *Rallus elegans* generally are larger than those of *R. longirostris* (see measurements of humeri in Emslie 1992), but these two species cannot be distinguished by characters of postcranial elements. Nevertheless, the material from Inglis 1A most closely approximates the size of *R. longirostris* and may represent that species.

Rallus limicola Vieillot 1819

Referred material.—Lecanto 2A: right coracoid, UF 101488; left humerus, UF 101514; right femur, UF 101489.

Haile 16A: left coracoid, UF 31947; two right humeri, UF 31940, 31942; left humerus, UF 31943; distal left humerus, UF 31939; left carpometacarpus, UF 31944; proximal right tarsometatarsus, UF 105830; proximal left tarsometatarsus, UF 105829; three distal right tarsometatarsi, UF 105826–105828; two distal left tarsometatarsi, UF 31945, 105799.

Rallus sp. A

Referred material.—Haile 16A: humeral end left coracoid, UF 31946; distal left humerus, UF 31938; right humerus, UF 31941.

Rallus sp. B

Referred material.—Haile 7C: distal right tibiotarsus, UF 159401.

Inglis 1A: shaft left tibiotarsus, UF 30321; distal left tibiotarsus, UF 30322.

Description.—These elements, and those of *Rallus* sp. A, are of rails intermediate in size between *R. longirostris* and *R. limicola.* They may represent an undescribed species, but can be distinguished from modern North American *Rallus* only by their size (see Emslie 1992 for measurements). The material reported here falls within the size range of *Rallus* sp. A and B as reported from Macasphalt Shell Pit (Emslie 1992).

Rallus sp.

Referred material.—Haile 7C: distal right tarsometatarsus missing middle and internal trochleae, UF 159400.

Inglis 1C: left radius, UF 165584.

Discussion.—UF 159400 is too fragmentary for specific identification; UF 165584 is intermediate in size between the smaller *Rallus limicola* and the larger *R. elegans* and *R. longirostris,* and it probably represents either *Rallus* sp. A or B.

Porzana carolina (Linnaeus 1758)

Referred material.—Lecanto 2A: premaxilla, UF 101533.

Inglis 1A: left carpometacarpus, UF 30312; two distal right tibiotarsi, UF 30314, 30315.

Porphyrula martinica (Linnaeus 1766)

Referred material.—Cutler Hammock: proximal left humerus, UF 159208.

Fulica americana Gmelin 1789

Referred material.—Cutler Hammock: two sternal left coracoids, UF 159224, 159225; proximal left humerus, UF 159089; proximal left ulna, UF 102207; distal right tibiotarsus, UF 102206; proximal half left tarsometatarsus, UF 159213.

D&M Shell Pit: right coracoid, UF 159455; two proximal left tarsometatarsi, UF 159454, 159460.

Forsberg Shell Pit: proximal right tibiotarsus, UF 159439; two distal left tibiotarsi, UF 159442, 159443.

Pelican Road Shell Pit: distal left femur, UF 159594; two distal right tibiotarsi, UF 159596, 159597; distal left tibiotarsus, UF 159595.

Discussion.—*Fulica americana* commonly occurs in the fossil record of Florida. It also is known from Macasphalt Shell Pit where the small temporal form recognized is the earliest record of the American Coot in North America (Emslie 1992).

Family GRUIDAE

Grus americana (Linnaeus 1758)

Referred material.—Inglis 1A: proximal right ulna missing olecranon, UF 30049.

Measurements.—UF 30049 measures proximal breadth, 23.0, breadth and depth of shaft at nutrient foramen, 12.2 and 10.2.

Description.—UF 30049 compares well in size and characters with the living species. Specifically, the attachment for the anterior articular ligament is long and narrow in UF 30049 and *Grus americana* (this attachment is shorter and broader in *G. canadensis*).

Discussion.—This specimen is the earliest fossil record of *Grus americana.* Within Florida, specimens also have been reported from West Palm Beach, Ichetucknee River, and Aucilla River (McCoy 1963; Olson 1972; Campbell 1980; Becker 1985a). Whooping Cranes occurred historically in Florida, but it is unknown if these birds were migrants or residents (Robertson and Woolfenden 1992) and there are no known breeding records (Stevenson and Anderson 1994). The Inglis 1A record indicates that this species has occurred in Florida since the late Pliocene.

Grus sp.

Referred material.—Shell Materials Pit: distal left tibiotarsus, UF 91223.

Description.—This specimen is from a large crane that probably represents an undescribed species (see Emslie 1995a for measurements and discussion).

Family PHORUSRHACIDAE

Titanis walleri Brodkorb 1963

Referred material.—Inglis 1A: two cervical vertebrae, UF 30005, 30006; left carpometacarpus, UF 30003; shaft right tibiotarsus, UF 30002; partial metatarsal I, UF 30007; left phalanx I of digit III, UF 30001; left phalanx II of digit III, UF 30010; left phalanx III of digit III, UF 30011; right phalanx I of digit IV, UF 30008; left phalanx I of digit IV, UF 30009.

Discussion.—This large flightless bird represents a family with a long fossil history in South America beginning in the Oligocene. Originally described on the basis of a distal right tarsometatarsus (UF 4108), *Titanis walleri* has been reported from only two other late Pliocene localities in Florida, at Port Charlotte, Charlotte County, and the Sante Fe River (the type locality), Gilchrist–Columbia County (Brodkorb 1963a; Chandler 1994). The youngest record for *T. walleri* is from late Pleistocene (Rancholabrean) deposits on the coastal plain of south Texas (Baskin 1995).

Order CHARADRIIFORMES

Family CHARADRIIDAE

Vanellus chilensis (Molina 1782)

Referred material.—Arredondo 2A: distal left humerus, UF/PB 1712; proximal right humerus, UF/PB 1713.

Description.—These specimens were originally described by Brodkorb (1959) as the type material for an extinct genus and species of lapwing, *Dorypaltus prosphatus,* known only from the late Pleistocene Arredondo 2A. The generic diagnosis was based on the smaller size and longer ectepicondylar process of UF/PB 1712 compared to *Vanellus chilensis* (Brodkorb 1959). I found the two fossil specimens to fall within the size and range of variation of humeri from four modern specimens of *V. chilensis* at FLMNH. In particular, the length of the ectepicondylar process and size and shape of the impression for the M. brachialis anticus vary considerably in the living species. In UF/PB 1713, the internal tuberosity is smaller and less robust than in the living species. Thus, the generic characters for *Dorypaltus* given by Brodkorb (1959) are not considered valid. In general, I found the fossil specimens to differ from *V. chilensis* only in their smaller size as discussed by Brodkorb (1959). As I do not consider size alone to be a valid character on which to base a fossil species, *D. prosphatus* is hereby considered to be synonymous with *V. chilensis.*

This systematic decision necessitates the removal of six specimens referred to *Dorypaltus prosphatus* from Haile 11B (Ligon 1965) to *Vanellus chilensis.* Three of these specimens, a proximal right humerus (UF 7175), proximal right femur (UF 7176A), and distal right tibiotarsus (UF 7177C) also were found to compare well to *V. chilensis* except for their slightly smaller size. Of the remaining three specimens, a proximal left femur (UF 7176B) is an indeterminate Charadriiformes, whereas a humeral left coracoid (UF 7174) and distal right tibiotarsus (UF 7177A) figured by Ligon (1965, fig. 4c–e) could not be located in the collections at FLMNH.

Discussion.—The referral of these specimens to *Vanellus chilensis* does not alter the significance of lapwings inhabiting Florida in the late Pleistocene. This species currently occurs in savannah and grassland regions in Central and South America. It apparently expanded its range northward into North America, perhaps during a glacial stage when a lowering of sea level increased the extent of the Gulf Coast habitat corridor (see Discussion below). One other North American record of a lapwing from the late Pleistocene Rancho La Brea, California, is under study (K. Campbell, pers. comm.).

Family JACANIDAE

Jacana spinosa (Linnaeus 1758)

Referred material.—Lecanto 2A: distal right tibiotarsus, UF 101534.

Discussion.—*Jacana spinosa* has been reported from only one other locality in Florida, Leisey Shell Pit 2 (Emslie 1995a). A large, extinct species (*J. farrandi*) is known from the late Miocene of Florida (Olson 1976b; Becker 1987a). Jacanas do not occur in Florida today.

Family SCOLOPACIDAE

cf. *Tringa* sp.

Referred material.—Inglis 1C: distal right tarsometatarsus, UF 165521.

Catoptrophorus semipalmatus (Gmelin 1789)

Referred material.—Haile 7C: distal right tibiotarsus, UF 159392.

Discussion.—This specimen is the first pre-Holocene record of *Catoptrophorus semipalmatus* in Florida and the earliest record in North America. The Willet has been reported from one archaeological site in Florida (Brodkorb 1967). It commonly occurs in the state today, frequenting coastal areas, and breeds in grasslands and marshlands (Stevenson and Anderson 1994).

Calidris cf. *C. pusilla* (Linnaeus 1766)

Referred material.—Lecanto 2A: right humerus, UF 101484; left humerus, UF 101485; right ulna, UF 101522; proximal left ulna, UF 101486; proximal left femur, UF 101515.

Description.—These specimens are tentatively referred to *Calidris pusilla* because bones of the Western Sandpiper (*Calidris mauri*) overlap in size with those of *C. pusilla.*

Discussion.—This specimen is the first fossil record in Florida of Semipalmated Sandpiper, a regular migrant to both coasts today (Stevenson and Anderson 1994).

Limnodromus scolopaceus (Say 1823)

Referred material.—Cutler Hammock: left humerus missing proximal end, UF 159202.

Haile 16A: right coracoid, UF 31923.

Haile 7C: left ulna, UF 159394; left carpometacarpus, UF 159393.

Description.—These specimens are distinguished from the Short-billed Dowitcher (*Limnodromus griseus*) by their generally larger size, which is similar to that of *L. scolopaceus.*

Discussion.—The specimens from Haile 16A and 7C are the earliest fossil record of *Limnodromus scolopaceus,* which also has been reported from the late Pleistocene of Rock Springs, Florida (Woolfenden 1959).

Gallinago gallinago (Linnaeus 1758)

Referred material.—Cutler Hammock: distal right humerus, UF 101545.

Inglis 1A: right humerus, UF 30327; three proximal right humeri, UF 30328–30330; left humerus missing proximal end, UF 30332; distal left humerus, UF 30331; two left carpometacarpi, UF 30333, 30334; right tarsometatarsus, UF 30335; distal left tarsometatarsus, UF 30336.

Inglis 1C: left humerus, UF 165545.

Discussion.—The specimens from Inglis 1A and 1C are the earliest fossils reported for *Gallinago gallinago,* which also is known from the late Pleistocene Haile 11B (Ligon 1965) and Reddick localities (Brodkorb 1957).

Scolopax minor Gmelin 1789

Referred material.—Cutler Hammock: right coracoid missing proximal head, UF 159276.

Discussion.—*Scolopax minor* also has been reported from the middle Pleistocene Coleman 2A (Ritchie 1980) and the late Pleistocene Haile 11B (Ligon 1965) and Eichelberger Cave (Brodkorb 1956b), Florida.

Scolopax hutchensi, new species
(Fig. 12A)

Holotype.—Complete left humerus, UF 165526.

Type locality and age.—Inglis 1C, Citrus County, Florida.

Paratypes.—Haile 16A: distal right tibiotarsus, UF 102398.

Inglis 1A: proximal right scapula, UF 30348; right coracoid, UF 30337; humeral right coracoid, UF 30338; proximal right ulna, UF 30340; synsacrum, UF 30341; distal right femur, UF 30342; two distal right tibiotarsi, UF 30343, 30344; right tarsometatarsus, UF 30346; right tarsometatarsus missing distal end, UF 30345; left tarsometatarsus, UF 30347.

Inglis 1C: right scapula, UF 165541; two right coracoids, UF 165525, 165551; left ulna, UF 165566; left ulna missing proximal end, UF 165574; left tarsometatarsus, UF 165528; two right tarsometatarsi, UF 165527, 165537 (Fig. 12B).

Macasphalt Shell Pit: left coracoid, UF 94942.

Measurements.—See Tables 9 and 10.

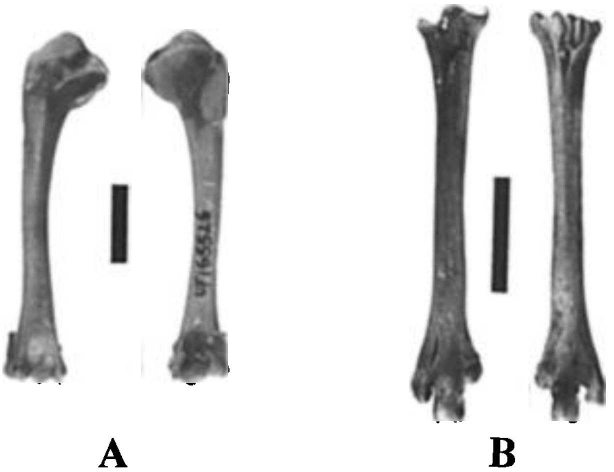

FIG. 12. (*A*) Anconal (left) and palmar (right) views of the holotype left humerus (UF 165526) of *Scolopax hutchensi*, new species, from Inglis 1C, Florida. Scale 1×; bar = 1 cm. (*B*) Anterior (left) and posterior (right) views of the paratype right tarsometatarsus (UF 165537) of *Scolopax hutchensi*, new species, from Inglis 1C, Florida. Scale 1.5×; bar = 1 cm.

Diagnosis.—Humerus intermediate in size and robustness between the larger *Scolopax rusticola* and smaller *S. minor* and *S. anthonyi* (Tables 9, 10; Olson 1976c, table 1); scar for pectoral attachment broad and does not extend as far distad on shaft (attachment narrower and extends farther distad on shaft in *S. minor* and *S. rusticola*); ectepicondylar ridge extends farther proximad on shaft than in *S. minor* and *S. anthonyi*, similar to *S. rusticola*; impression of M. brachialis anticus broad and rounded (impression longer and narrower in *S. minor*, *S. anthonyi*, and *S. rusticola*); attachment for anterior articular ligament long and narrow (attachment rounded and broader in *S. minor* and *S. rusticola*); entepicondyle larger and more pronounced in distal view than in *S. minor* and is similar to *S. rusticola* (Fig. 12A).

Compared to the bones of *Scolopax minor*, those of the new species are distinguished as follows: coracoid with longer, narrower shaft; muscle scar below procoracoid smaller and higher on shaft; glenoid facet large. Ulna with prominence for anterior articular ligament larger and more robust; small papilla for bicipital attachment more pronounced and nearly separate from external cotyla; distal palmar border of external cotyla angled distad to midshaft (border curves sharply to midshaft in *S. minor*); internal condyle blunter and more robust; proximal end of external condyle broader and extends farther up shaft. Scapula with head of coracoidal articulation larger. Tibiotarsus with long muscle scar on anterior distal shaft above external condyle (scar shorter in *S. minor*); distal surface of internal condyle with low shelf (surface has distinct raised shelf in *S. minor*); internal condyle less robust (condyle more robust in *S. minor*); greater excavation on the lateral surface of the external condyle and on the internal surface of the internal condyle (both areas shallowly excavated in *S. minor*); papilla for muscle attachment on the internal side of the distal anterior shaft is positioned high on the shaft (papilla lower on shaft in *S. minor*). Tarsometatarsus with robust intercotylar prominence (Fig. 12B; prominence less robust in *S. minor*).

TABLE 9. Measurements (mm) of humeri of modern woodcocks and the fossil *Scolopax hutchensi*, new species, from Florida.*

Species	L	PB	PD	LBS	LDS	DB	DD
Scolopax minor (*n* = 10♂)							
Mean ± SD	40.8 ± 0.5	10.0 ± 0.1	3.3 ± 0.2	3.2 ± 0.1	2.7 ± 0.1	7.3 ± 0.1	4.4 ± 0.1
Range	39.9–41.6	9.8–10.2	3.0–3.6	3.0–3.3	2.6–2.9	7.1–7.5	4.3–4.6
Scolopax minor (*n* = 10♀)							
Mean ± SD	43.8 ± 1.0	10.7 ± 0.4	3.3 ± 0.1	3.4 ± 0.2	2.9 ± 0.2	7.7 ± 0.3	4.6 ± 0.2
Range	41.4–45.0	10.0–11.4	3.1–3.5	3.1–3.9	2.6–3.1	7.3–8.1	4.3–5.0
Scolopax rusticola (*n* = 10; 3♂, 3♀, 4?)							
Mean ± SD	55.1 ± 0.9	13.6 ± 0.4	4.5 ± 0.2	4.4 ± 0.2	3.8 ± 0.2	9.8 ± 0.2	6.1 ± 0.2
Range	53.4–56.3	13.1–14.3	4.2–4.9	4.1–4.6	3.3–4.0	9.5–10.1	5.9–6.4
Scolopax hutchensi							
UF 165526	48.2	11.6	3.7	3.7	3.3	8.6	5.4

* L = length; PB = proximal breadth; LBS = least breadth shaft; LDS = least depth shaft; DB = distal breadth; DD = distal depth.

TABLE 10. Measurements (mm) of tarsometatarsi of modern woodcocks and fossils of *Scolopax hutchensi*, new species, from Florida.*

Species	L	PB	PD	LBS	LDS	DB	MTB	MTD
Scolopax minor (*n* = 10♂)								
Mean ± SD	31.0 ± 0.6	5.3 ± 0.1	5.5 ± 0.2	2.0 ± 0.1	1.8 ± 0.1	5.5 ± 0.2	2.1 ± 0.03	2.9 ± 0.1
Range	29.9–31.6	5.2–5.4	5.2–5.9	1.9–2.3	1.7–1.8	5.3–5.9	2.1–2.2	2.8–3.0
Scolopax minor (*n* = 10♀)								
Mean ± SD	33.9 ± 1.2	5.6 ± 0.2	5.9 ± 0.3	2.4 ± 0.2	1.9 ± 0.1	5.9 ± 0.3	2.3 ± 0.1	3.2 ± 0.2
Range	31.1–35.3	5.2–5.8	5.6–6.3	1.9–2.6	1.8–2.1	5.4–6.2	2.1–2.5	2.9–3.5
Scolopax rusticola (*n* = 10; 3♂, 3♀, 4?)								
Mean ± SD	38.6 ± 1.6	7.1 ± 0.3	7.3 ± 0.3	3.0 ± 0.3	2.3 ± 0.1	7.2 ± 0.3	2.7 ± 0.1	3.9 ± 0.2
Range	36.0–40.8	6.6–7.6	6.9–8.1	2.6–3.4	2.2–2.5	6.8–7.7	2.5–2.8	3.6–4.0
Scolopax hutchensi								
UF 165527	33.5	6.2	6.2	2.6	2.0	5.6	2.5	3.0
UF 165528	32.3	6.4	6.2	2.7	2.2	6.4	2.4	3.4
UF 165537	37.1	6.6	6.7	2.8	2.1	6.5	2.4	3.6
UF 30345	—	6.8	6.7	2.7	—	—	—	—
UF 30346	35.9	—	—	2.7	2.1	5.8	2.3	3.3
UF 30347	36.2	6.3	—	2.6	2.1	6.4	2.2	3.3

* L = length; PB = proximal breadth; PD = proximal depth; LBS = least breadth shaft; LDS = least depth shaft; DB = distal breadth; MTB = middle trochlea breadth; MTD = middle trochlea depth.

Description.—These specimens are most similar in size and characters to females of *Scolopax minor* (*n* = 5, USNM; Tables 9, 10). *Scolopax hutchensi* appears to have had larger, more robust wing bones relative to its leg elements, the latter being similar to those in *S. minor,* the only living congeneric species in North America today.

One bone, a coracoid (UF 94942), was referred to *Scolopax* sp. from Macasphalt Shell Pit by Emslie (1992). This specimen is more similar to *S. minor* than to *S. hutchensi* in size, but shares characters with the latter species in having a scar below the procoracoid small and high on shaft compared to the former. Based on these similarities, UF 94942 is herein referred to *S. hutchensi.*

Etymology.—Named for Steve Hutchens, who discovered the type locality and donated fossil material to FLMNH, in recognition of his contributions to Florida paleontology.

Discussion.—This is only the second fossil species of *Scolopax* to be described. Wetmore (1920) described *Gallinago anthonyi* from late Pleistocene cave deposits in Puerto Rico. This material was restudied by Olson (1976c) who determined that the fossils actually represent an extinct woodcock, which he referred to *S. anthonyi.* Based on character descriptions, measurements, and illustrations of a paratype humerus (AMNH 2909) provided by Olson (1976c, fig. 1, table 1), *S. anthonyi* differs from *S. hutchensi* by its generally smaller humerus and other characters of this element listed above, more robust coracoid and tarsometatarsus, and longer and narrower shaft of the tibiotarsus. One other fossil species, *S. ghardalamensis* from the Pleistocene of Malta, was restudied by Olson (1976c) who found that it is not a woodcock and actually represents *Coturnix coturnix.* The geochronologic range of *S. hutchensi* is from the late Pliocene through early Pleistocene (2.4–1.0 Ma).

Charadriiformes, indeterminate

Referred material.—Cutler Hammock: distal right tarsometatarsus, UF 159201. Inglis 1A: distal left humerus, UF 30339.

Order COLUMBIFORMES

Family COLUMBIDAE

Columba fasciata Say 1823

Referred material.—Lecanto 2A: right tarsometatarsus, UF 101492.

Description.—This specimen compares well in size and characters to the living species, except for a slightly broader distal end (Table 11). It differs from the tarsometatarsus in *Zenaida asiatica, Z. aurita, Z. macroura,* and *Ectopistes migratorius* by its larger size and more robust shaft, and from *Staroenas cyanocephalus* by its shorter, more robust shaft and longer (proximo-distally) trochleae. UF 101492 and tarsometatarsi of modern *C. fasciata* differ from those of *C. leucocephala* in having a longer and more robust shaft (Table 11), metatarsal facet placed lower on shaft, and hypotarsus that extends farther posteriad (shaft narrower, metatarsal facet higher, and hypotarsus not extending as far posteriad in *C. leucocephala*). In *C. squamosa* the proximal and distal ends are broader and deeper, the middle trochlea is broader (Table 11), the anterior metatarsal groove is shallower, and the metatarsal facet is higher on the shaft than in UF 101492 and modern *C. fasciata.* Other North American species (as recognized by the

TABLE 11. Measurements (mm) of tarsometatarsi of modern pigeons and the fossil of *Columba fasciata* (UF 101492) from Lecanto 2A, Florida.*

Species	L	PB	PD	LBS	LDS	DB	MTB	MTD
Columba fasciata (*n* = 8♂)								
Mean ± SD	27.6 ± 1.4	7.2 ± 0.3	6.8 ± 0.3	3.3 ± 0.1	2.2 ± 0.1	6.8 ± 0.2	2.3 ± 0.1	3.0 ± 0.2
Range	26.0–30.3	6.7–7.6	6.3–7.3	3.0–3.5	2.0–2.3	6.6–7.2	2.3–2.5	2.8–3.3
Columba fasciata (*n* = 5♀)								
Mean ± SD	27.1 ± 0.7	7.0 ± 0.3	6.5 ± 0.3	3.1 ± 0.2	2.2 ± 0.1	6.8 ± 0.4	2.2 ± 0.1	3.0 ± 0.2
Range	26.4–27.9	6.4–7.4	6.0–6.8	2.9–3.3	2.0–2.3	6.2–7.2	2.0–2.3	2.7–3.2
UF 101492	28.0	7.2	6.8	3.5	2.4	7.5	2.5	3.0
Columba leucocephala (*n* = 3♂, 2♀, 2?)								
Mean ± SD	26.1 ± 0.7	6.9 ± 0.3	6.2 ± 0.4	3.1 ± 0.2	2.1 ± 0.1	6.9 ± 0.3	2.3 ± 0.1	2.9 ± 0.1
Range	25.2–27.2	6.4–7.5	5.4–6.7	2.8–3.3	2.0–2.2	6.3–7.3	2.1–2.5	2.7–3.0
Columba squamosa (*n* = 4♂, 2♀)								
Mean ± SD	27.8 ± 1.2	7.5 ± 0.1	7.2 ± 0.3	3.5 ± 0.2	2.4 ± 0.1	7.3 ± 0.5	2.6 ± 0.3	3.1 ± 0.3
Range	26.4–29.6	7.4–7.6	6.8–7.8	3.3–3.8	2.2–2.5	6.5–8.0	2.2–3.0	2.6–3.6
Columba cayennensis (*n* = 2♂, 3?)								
Mean ± SD	25.2 ± 1.1	6.4 ± 0.4	6.1 ± 0.2	3.0 ± 0.2	2.0 ± 0.1	6.5 ± 0.2	2.2 ± 0.1	2.6 ± 0.1
Range	23.6–26.8	5.9–7.0	5.8–6.4	2.7–3.3	1.9–2.2	6.3–6.9	2.1–2.3	2.5–2.8
Columba flavirostris (*n* = 1♂, 1♀, 4?)								
Mean ± SD	25.5 ± 1.8	6.5 ± 0.4	6.1 ± 0.4	3.0 ± 0.3	2.0 ± 0.2	6.2 ± 0.4	2.2 ± 0.2	2.6 ± 0.2
Range	23.0–28.5	5.9–7.3	5.5–6.6	2.7–3.4	1.8–2.3	5.7–6.7	1.9–2.4	2.4–3.0

* L = length; PB = proximal breadth; PD = proximal depth; LBS = least breadth shaft; LDS = least depth shaft; DB = distal breadth; MTB = middle trochlea breadth; MTD = middle trochlea depth.

AOU 1983) that approach the size of *C. fasciata* include *C. cayennensis, C. nigrirostris, C. subvinacea,* and *C. flavirostris,* all of which are smaller than *C. fasciata* (Table 11), and *C. picazuro,* which is larger. No specimens of *C. caribaea* or *C. inornata* were available for comparison.

Discussion.—This specimen is the first fossil record of *Columba fasciata* in the eastern USA. There are three modern records of Band-tailed Pigeon from Florida, all in fall or winter (Stevenson and Anderson 1994). The species indicates that a forested environment surrounded the Lecanto 2A fossil locality in the late Pleistocene.

Columba sp.

Referred material.—Inglis 1A: distal right humerus, UF 165569.

Inglis 1C: right scapula, UF 165586; humeral left coracoid, UF 165535.

Description.—These specimens represent a pigeon smaller and less robust than *Columba livia* and *C. fasciata,* and compare most closely in size to *C. cayenensis.* However, UF 165569 differs from *C. cayenensis* in having a longer internal condyle, a deeper fossa behind the internal condyle, and a more distal position of the lateral external papilla on the shaft. UF 165586 differs from *C. cayenensis* in having a smaller pneumatic foramen and UF 165535 has a smaller and less curved sternal border to the glenoid facet.

Discussion.—These specimens may represent an undescribed species, but they are too fragmentary to characterize adequately. They do, however, represent the earliest record of *Columba* in North America. The family first occurs in North America (in Florida) in the early Miocene (Becker and Brodkorb 1992).

Zenaida macroura (Linnaeus 1758)

Referred material.—Cutler Hammock: carina of sterna, UF 159099, 159236; right coracoid, UF 159245; right coracoid missing sternal end, UF 159235; humeral right coracoid, UF 159275; three humeral left coracoids, UF 102287, 159234, 159246; two left humeri, UF 102294, 159179; three proximal left humeri, UF 102290, 159071, 159240; four proximal right humeri, UF 102291, 159086, 159237, 159238; five distal right humeri, UF 102289, 102295, 159178, 159239, 159244; shaft left humerus, UF 102293; two distal left humeri, UF 159241, 159242; left carpometacarpus, UF 102292; proximal right tarsometatarsus, UF 159243; distal right tarsometatarsus, UF 102288.

Lecanto 2A: right humerus, UF 101493.

Haile 16A: right coracoid, UF 31901; two proximal left humeri, UF 31898, 31899; proximal right humerus, UF 31900.

Inglis 1A: proximal right scapula, UF 31421; proximal left scapula, UF 31420; left coracoid, UF 31414; left coracoid missing sternal end, UF 31413; two humeral left coracoids, UF 31417, 31418; sternal right coracoid, UF 31419; two left coracoids missing humeral ends, UF 31415, 31416; six carinae of sterna, UF 31397–31402; left humerus, UF 31409; proximal right humerus, UF 31403; proximal left humerus, UF 31411; right humerus missing proximal end, UF 31404; four right distal humeri, UF 31405–31408; left distal humerus, UF 31410; shaft left humerus, UF 31412; left ulna, UF 31431; proximal right ulna, UF 31428, proximal left ulna, UF 31433; two right distal ulnae, UF 31429, 31430; distal left ulna, UF 31432; proximal left radius, UF 31422; left ulnare, UF 30349; proximal right carpometacarpus, UF 30350; proximal left tibiotarsus, UF 31424; three distal left tibiotarsi, UF 31425–31427; right tarsometatarsus, UF 31423.

Inglis 1C: humeral end of right coracoid, UF 165608.

Discussion.—*Zenaida macroura* commonly occurs in the fossil record of Florida, as shown by the amount of material reported here and elsewhere (Brodkorb 1971). The specimens from Inglis 1A are the earliest records of the Mourning Dove in North America. One fossil species, *Zenaida prior,* is known by a proximal humerus from the late Pliocene of Rexroad, Kansas (Brodkorb 1969). It differs from *Z. macroura* as described by Brodkorb (1969).

cf. *Zenaida* sp.

Referred material.—Cutler Hammock: distal right humerus, UF 102298.

Measurements.—UF 102298 measures distal breadth, 8.7; depth at external condyle, 5.0.

Description.—This specimen is similar in size to a large species of *Zenaida,* and smaller than species in *Columba.* It compares best to *Z. asiatica* or *Z. aurita,* but it is not possible to distinguish these species by their distal humeri.

Discussion.—The Mourning Dove (*Zenaida macroura*) and Passenger Pigeon (*Ectopistes migratorius*) also are known from Cutler Hammock (see below). This specimen indicates that a third species of dove or pigeon is represented at this site, but additional material is needed for species determination.

cf. *Ectopistes migratorius* (Linnaeus 1766)

Referred material.—Cutler Hammock: anterior carina of sternum, UF 102296.

Description.—This specimen was compared to sterna of *Zenaida asiatica, Columba leucocephala, C. cayenensis, C. fasciata, C. speciosa, C. flavirostris,* and *Ectopistes migratorius.* UF 102296 is recognized as *E. migratorius* by the relative size and shape of the manubrium and thickness of the anterior carina. It compares well with six sterna (USNM 24828) of *E. migratorius* from the late Pleistocene Ladds Quarry, Georgia.

Discussion.—This is the fourth record of the Passenger Pigeon from Florida, and the most southern fossil record for the species. One specimen each also was referred to *Ectopistes migratorius* from the late Pleistocene of Rock Springs (Woolfenden 1959) and the Ichetucknee River (Campbell 1980), and six specimens from Haile 11B (Ligon 1965). Historically, the Passenger Pigeon has been reported as far south as Cuba (accidental; Schorger 1973).

Order CUCULIFORMES
Family CUCULIDAE

Coccyzus americanus (Linnaeus 1758)

Referred material.—Inglis 1A: three proximal left mandibles, UF 30285–30287; proximal left scapula, UF 30289; humeral left coracoid, UF 30288; two right proximal humeri, UF 30306, 30307; proximal left humerus, UF 30308; three distal right humeri, UF 30303–30305; shaft right humerus, UF 30309; left ulna, UF 30294; proximal right ulna, UF 30296; shaft left ulna, UF 30295; right carpometacarpus, UF 30293; proximal right tibiotarsus, UF 30297; two distal right tibiotarsi, UF 30301, 30302; three distal left tibiotarsi, UF 30298–30300; right tarsometatarsus, UF 30291; proximal right tarsometatarsus, UF 30292; proximal left tarsometatarsus, UF 30290.

Description.—These specimens compare well in size and characters to the living species.

Discussion.—This material represents the earliest fossil record of *Coccyzus americanus* in North America. It also has been reported from Haile 11B (Ligon 1965).

Order STRIGIFORMES

Family TYTONIDAE

Tyto alba (Scopoli 1769)

Referred material.—Cutler Hammock: proximal right tarsometatarsus, UF 159200; proximal left tarsometatarsus, UF 159168; distal left tarsometatarsus, UF 159204.

Haile 16A: two humeral right coracoids, UF 102370, 102371; humeral left coracoid, UF 102372; sternal right coracoid, UF 31959; proximal left scapula, UF 102374; proximal right scapula, UF 102373; distal left humerus, UF 31960; proximal right ulna, UF 102366; distal right ulna (juvenile), UF 102367; left carpometacarpus, UF 102369; proximal right carpometacarpus, UF 102368; distal right femur, UF 102375; three proximal fibulae, UF 102376–102378; proximal left tarsometatarsus, UF 31961.

McLeod Limerock Mine, Pocket A: right tibiotarsus, AMNH 27777.

Inglis 1A: proximal half left femur, UF 30173.

Family STRIGIDAE

Otus asio (Linnaeus 1758)

Referred material.—Cutler Hammock: distal right humerus, UF 102284; distal left humerus, UF 159226; proximal right carpometacarpus, UF 102281; distal right tibiotarsus, UF 159199; three distal left tibiotarsi, UF 159198, 159231, 159233; proximal right tarsometatarsus, UF 159228; two proximal left tarsometatarsi, 102283, 159229; four distal left tarsometatarsi, UF 102279, 102280, 159227, 159232; three distal right tarsometatarsi, UF 102282, 159101, 159230.

Lecanto 2A: right scapula, UF 101500; left scapula, UF 101502; left humerus missing proximal end, UF 101503; shaft left humerus, UF 101504; left tarsometatarsus, UF 101505; left tarsometatarsus missing middle and internal trochleae, UF 101506; distal right tarsometatarsus, UF 101507.

Haile 16A: humeral right coracoid, UF 31964; two distal right humeri, UF 31962, 31963; two distal right tibiotarsi, UF 31967, 31968; distal left tibiotarsus, UF 31969; two distal left tarsometatarsi, UF 31965, 31966.

Inglis 1A: two proximal right scapulae, UF 30199, 30200; right coracoid, UF 30203; left coracoid, UF 30202; humeral right coracoid, UF 30204; sternal left coracoid, UF 30201; proximal right humerus, UF 30233; two shafts right humeri, UF 30234, 30235; two proximal left humeri, UF 30228, 30229; shaft left humerus, UF 30232; left humerus missing distal end, UF 30227; three distal right humeri, UF 30236–30238; two distal left humeri, UF 30230, 30231; distal left ulna, UF 30208; proximal right radius, UF 30207; distal right radius, UF 30206; distal left radius, UF 30205; right carpometacarpus, UF 30198; left carpometacarpus, UF

30196; right femur, UF 30212; two proximal right femora, UF 30210, 30211; two distal right femora, UF 30213, 30214; proximal right tibiotarsus, UF 30215; four distal right tibiotarsi, UF 30217–30220; left tibiotarsus missing proximal end, UF 30216; right tarsometatarsus, UF 30226; two left tarsometatarsi, UF 30223, 30224; distal right tarsometatarsus, UF 30225; distal left tarsometatarsus, UF 30222; pedal phalanx, UF 30221.

Inglis 1C: distal left tibiotarsus, UF 165568.

Discussion.—Otus asio commonly occurs in the fossil record of Florida as indicated by the amount of material reported here and from several other late Pleistocene sites in the state. The specimens from Inglis 1A represent the earliest fossil occurrence of *O. asio* in Florida.

Bubo virginianus (Gmelin 1788)

Referred material.—Cutler Hammock: distal left humerus, UF 159177; distal left ulna, UF 159073.

Inglis 1A: right humerus with ends damaged, UF 30159; right ulna, UF 30160; left ulnare, UF 30158; proximal right femur, UF 30161; distal left radius, UF 30162; right acetabulum, UF 30163; distal right tibiotarsus, UF 30166; two distal left tibiotarsi, UF 30164, 30165; two pedal phalanges, UF 30176, 30177.

Description.—This material compares well in size and features to the living species. Only one fossil species of the genus, *Bubo sinclairi* from the late Pleistocene of California and Utah (Miller 1911b; Emslie and Heaton 1987), is known from North America. This species, however, was much larger than *B. virginianus.*

Discussion.—Bubo virginianus also has been reported from the Irvingtonian sites at Leisey 1A and Coleman 2A, Florida (Ritchie 1980; Emslie 1995a). Although *B. virginianus* is well known from late Pleistocene and Holocene sites in western North America (Brodkorb 1971), the record from Cutler Hammock is the first from the dozens of localities of this age in Florida. The Great Horned Owl is a common resident throughout much of the state today (Stevenson and Anderson 1994).

Glaucidium explorator, new species

(Fig. 13B)

Holotype.—Left tarsometatarsus, UF 30185.

Type locality and age.—Inglis 1A, Sec. 8, T17S, R16E, Citrus County, Florida; late Pliocene (early Irvingtonian), 2.0–1.6 Ma (Morgan and Hulbert 1995).

Paratypes.—Two proximal right scapulae, UF 30189, 30190; proximal right humerus, UF 30192; proximal right femur, UF 30183; left femur, UF 30187; distal left femur, UF 30188; right tibiotarsus, UF 30193 (Fig. 13A); two distal left tibiotarsi, UF 30194, 30195; shaft left tibiotarsus, UF 30191; proximal left tarsometatarsus, UF 30186; distal right tarsometatarsus, UF 30184.

Measurements.—See Tables 12 and 13.

Diagnosis.—Tarsometatarsus (UF 30184–30186) distinguished as a species of *Glaucidium* by shaft short and begins to flare outward to proximal end at midshaft, tubercle for tibialis anticus placed low on anterior shaft, and distal tendinal opening placed near to external trochlea (Fig. 13B; shaft longer and narrower with tubercle positioned higher on shaft in *Aegolius*; shaft begins flaring nearer proximal end in *Ciccaba, Micrathene, Pseudoscops, Rhinoptynx, Ninox, Asio,*

FIG. 13. Anterior (left) and posterior (right) views of (*A*) the paratype right tibiotarsus (UF 30193) and (*B*) holotype left tarsometatarsus (UF 30185) of *Glaucidium explorator*, new species, from Inglis 1A, Florida. Scale 2×; bar = 1 cm.

Strix, Athene, Pulsatrix, Nyctea, Otus, Tyto, and ***Bubo***; shaft shorter and more robust in ***Surnia***; and distal tendinal opening farther from external trochlea in ***Pseudoscops, Rhinoptynx, Pulsatrix, Nyctea, Bubo,*** and ***Otus***). Femur (UF 30183, 30187, 30188) recognized as ***Glaucidium*** by short neck leading to head, in proximal view, and shallow fibular groove (neck longer in ***Aegolius*** and ***Micrathene***; and groove deep in ***Aegolius***). Tibiotarsus (UF 30191, 30193, 30195) recognized as ***Glaucidium*** by weakly developed shelf at groove for peroneus profundus, papilla for muscle attachment at distal internal shaft positioned low on shaft, and distal anterior shaft deeply excavated (Fig. 13A; shelf well developed to moderately developed in ***Aegolius*** and ***Micrathene***; distal papilla higher on shaft in ***Micrathene, Athene, Ninox, Strix, Pseudoscops, Rhinoptynx, Ciccaba, Pulsatrix, Bubo, Tyto,*** and ***Otus***; and shaft only shallowly excavated in ***Aegolius, Micrathene, Ciccaba, Surnia, Tyto,*** and ***Otus***).

Tarsometatarsus (UF 30185) differs from that of other species of ***Glaucidium*** by straight, robust shaft (shaft narrower in ***G. gnoma*** and ***G. siju,*** longer with broader distal end in ***G. brasilianum,*** and flares outward above mid-shaft in ***G. gnoma, G. brasilianum, G. siju, G. brodiei,*** and ***G. perlatum***; Table 13), distal tendinal opening positioned near external trochlea (opening positioned farther from external trochlea in ***G. siju*** and ***G. brasilianum***), and in distal view the internal trochlea is positioned more anteriad (trochlea positioned farther posteriad in ***G. siju, G. brasilianum, G. brodiei,*** and ***G. passerinum***). Femur (UF 30187) longer than that in ***G. gnoma, G. siju, G. brasilianum,*** and ***G. minutissimum*** (Table 12) and with shorter neck from shaft to head in proximal view (neck longer in

TABLE 12. Measurements (mm) of femora and tibiotarsi of modern pygmy-owls and fossils of *Glaucidium explorator*, new species, and *Glaucidium* sp. from Florida.*

Element/species	L	PB	PD	LBS	LDS	DB	DD
Femur							
Glaucidium gnoma (*n* = 2♂, 5♀, 2?)							
Mean ± SD	27.1 ± 1.1	5.3 ± 0.2	3.4 ± 0.1	2.2 ± 0.1	2.2 ± 0.1	5.3 ± 0.2	4.4 ± 0.2
Range	24.7–28.4	5.0–5.5	3.2–3.5	2.0–2.4	2.0–2.4	5.1–5.7	4.1–4.7
Glaucidium brasilianum (*n* = 3♂, 7♀, 5?)							
Mean ± SD	29.1 ± 1.8	5.8 ± 0.4	3.6 ± 0.2	2.5 ± 0.2	2.4 ± 0.2	5.8 ± 0.4	4.7 ± 0.3
Range	26.4–32.8	5.1–6.6	3.2–4.0	2.1–2.9	2.1–2.8	5.1–6.7	4.3–5.4
Glaucidium siju (*n* = 1♂, 1♀, 1?)							
Mean ± SD	28.0 ± 1.3	5.2 ± 0.4	3.3 ± 0.2	2.2 ± 0.1	2.2 ± 0.1	5.3 ± 0.3	4.4 ± 0.2
Range	26.8–29.8	4.7–5.5	3.0–3.4	2.1–2.4	2.1–2.3	5.0–5.6	4.2–4.7
Glaucidium minutissimum (*n* = 2♂, 1♀)							
Mean ± SD	26.1 ±1.1	5.1 ± 0.3	3.3 ± 0.2	2.1 ± 0.1	2.1 ± 0.2	5.1 ± 0.3	4.3 ± 0.3
Range	24.9–27.0	4.8–5.3	3.1–3.4	2.0–2.2	1.9–2.3	4.8–5.3	4.0–4.6
Glaucidium explorator							
UF 30183	—	5.3	3.4	2.3	2.2	—	—
UF 30187	29.9	5.8	3.5	2.7	2.5	5.9	4.7
UF 30188	—	—	—	—	—	5.6	4.2
Tibiotarsus							
Glaucidium gnoma (*n* = 4♀, 1?)							
Mean ± SD	38.7 ± 0.6	4.5 ± 0.2	5.1 ± 0.1	2.2 ± 0.2	1.5 ± 0.1	4.9 ± 0.2	4.4 ± 0.2
Range	37.9–39.4	4.2–4.7	4.9–5.3	1.9–2.5	1.4–1.6	4.6–5.2	4.0–4.8
Glaucidium brasilianum (*n* = 3♂, 3♀, 5?)							
Mean ± SD	4.9 ± 2.9	4.7 ± 0.2	5.5 ± 0.4	2.4 ± 0.2	1.8 ± 0.2	5.4 ± 0.4	4.7 ± 0.3
Range	38.4–48.0	4.3–5.0	5.0–6.4	2.1–2.9	1.6–2.1	4.8–6.1	4.3–5.2
Glaucidium siju (*n* = 1♂, 1♀, 1?)							
Mean ± SD	39.6 ± 1.6	4.4 ± 0.3	5.0 ± 0.2	2.5 ± 0.2	1.6 ± 0.1	4.9 ± 0.2	4.2 ± 0.2
Range	38.4–41.9	4.1–4.7	4.8–5.2	2.2–2.8	1.4–1.7	4.6–5.1	3.9–4.4
Glaucidium explorator							
UF 30193	40.3	4.4	4.9	2.6	2.2	5.1	4.1
UF 30195	—	—	—	—	—	5.3	3.8
Glaucidium sp.							
UF 30181	35.8	—	—	2.2	1.8	4.3	3.1
UF 30182	—	4.1	4.9				

* L = length; PB = proximal breadth; PD = proximal depth; LBS = least breadth shaft; LDS = least depth shaft; DB = distal breadth; DD = distal depth.

TABLE 13. Measurements (mm) of tarsometatarsi of modern pygmy-owls and *Glaucidium explorator*, new species, from Inglis 1A, Florida.*

Species	L	PB	PD	LBS	LDS	DB	MTB	MTD
Glaucidium gnoma (*n* = 1♂, 4♀, 1?)								
Mean ± SD	19.5 ± 0.9	5.3 ± 0.2	5.0 ± 0.2	2.9 ± 0.1	1.8 ± 0.1	5.5 ± 0.1	2.6 ± 0.1	2.7 ± 0.2
Range	17.7–20.2	5.0–5.6	4.5–5.2	2.8–3.1	1.6–1.8	5.2–5.6	2.5–2.7	2.3–3.1
Glaucidium brasilianum (*n* = 3♂, 4♀, 5?)								
Mean ± SD	21.6 ± 1.6	5.8 ± 0.4	5.5 ± 0.4	3.2 ± 0.2	1.9 ± 0.3	6.0 ± 0.3	2.7 ± 0.2	3.0 ± 0.3
Range	19.8–24.6	5.0–6.4	4.9–6.4	2.9–3.5	1.6–2.4	5.4–6.6	2.4–3.1	2.4–3.4
Glaucidium siju (*n* = 1♂, 1♀, 1?)								
Mean ± SD	20.2 ± 0.8	5.3 ± 0.3	4.9 ± 0.3	3.0 ± 0.2	1.7 ± 0.1	5.5 ± 0.3	2.4 ± 0.2	2.7 ± 0.1
Range	19.7–21.3	4.9–5.6	4.5–5.3	2.7–3.2	1.5–1.8	5.1–5.8	2.3–2.7	2.5–2.8
Glaucidium explorator								
UF 30184	—	—	—	2.9	1.8	5.3	2.2	2.3
UF 30185	19.9	—	—	3.3	1.9	5.4	2.4	2.7
UF 30186	—	5.2	4.7	—	—	—	—	—

* L = length; PB = proximal breadth; PD = proximal depth; LBS = least breadth shaft; LDS = least depth shaft; DB = distal breadth; MTB = middle trochlear breadth; MTD = middle trochlear depth.

FIG. 14. Anterior view of left tibiotarsus (UF 30181) of *Glaucidium* sp. from Inglis 1A, Florida. Scale 2×; bar = 1 cm.

G. gnoma, G. brasilianum, G. brodiei, G. cuculoides, and *G. perlatum*). Tibiotarsus (UF 30193) with long outer cnemial crest that does not extend as far distad as in *G. gnoma, G. siju, G. brasilianum, G. jardinii, G. brodiei, G. cuculoides, G. perlatum,* and *G. passerinum*; shaft robust (shaft more slender in *G. gnoma, G. siju,* and *G. brasilianum*; Table 12); and papilla for muscle attachment on distal internal shaft positioned low (papilla higher on shaft in *G. siju, G. brasilianum,* and *G. perlatum*). No features were noted in the proximal scapula (UF 30189, 30190) and proximal humerus (UF 30192) that would distinguish them from those of modern pygmy-owls.

Etymology.—From Latin, *explorator,* masculine, for searcher or investigator, in reference to the location of this fossil species far outside the range of living pygmy-owls.

Discussion.—This material represents the first fossil species of *Glaucidium* to be described and the first pygmy-owl to be recorded in eastern North America. Three living species (*G. gnoma, G. minutissimum, G. brasilianum*) occur in western North America and Mexico, and one occurs in Cuba (*G. siju*). The origin of this group of small owls may be from tropical South and Central America, where most species occur today. If so, *G. explorator* may have reached Florida from the tropics along the Gulf Coast corridor during the Great American Interchange in the late Pliocene.

Glaucidium sp.

Referred material.—Inglis 1A: left tibiotarsus with damaged proximal end, UF 30181 (Fig. 14); proximal left tibiotarsus, UF 30182.

Measurements.—See Table 12.

Description.—These fossils are from a small pygmy-owl most similar in size to *Glaucidium minutissimum palmarum.* UF 30181 and UF 30182 differ from *G. minutissimum* in having a longer outer cnemial crest and fibular crest (Fig. 14).

Discussion.—This material probably represents an undescribed species of small pygmy-owl, but additional material is needed for its diagnosis and description. With *Glaucidium explorator* above, these two species of pygmy-owls may reflect a former forested or open woodland habitat surrounding Inglis 1A during the late Pliocene. The Least Pygmy-Owl (*G. minutissimum*) currently occurs in dense tropical forest and open scrubland, whereas the Ferruginous Pygmy-Owl (*G. brasilianum*) prefers woodlands and riparian regions and open scrubland and desert (Ginn 1973; de la Torre 1990).

Speotyto cunicularia (Molina 1782)

Referred material.—Inglis 1A: premaxilla, UF 30167; sternal half left coracoid, UF 30170; proximal right femur, UF 30172; left femur, UF 30169; distal left femur, UF 30168; distal left tibiotarsus, UF 30171.

Description.—These specimens compare well with the living species except for their slightly larger size and robustness. Ford (1966) described the fossil species *Speotyto megalopeza* from 11 partial elements, including the holotypical tarsometatarsus, five coracoids, a carpometacarpus, humerus, and quadrate, from the late Pliocene of Kansas. This species was distinguished by its larger size and greater robustness compared to living *S. cunicularia.* Later, Ford and Murray (1967) reported and assigned one other specimen, a distal radius, from Hagerman, Idaho, to *S. megalopeza.* Feduccia (1970) considered *S. megalopeza* to be synonymous with *S. cunicularia* and erected two new subspecies, *S. c. intermedia* and *S. c. megalopeza,* after restudying fossils reported by Ford (1966) and Ford and Murray (1967) and comparing these with a newly identified tarsometatarsus from the late Pliocene Sand Draw local fauna, Nebraska. Feduccia (1970) considered the two fossil subspecies to differ from living Burrowing Owls only by their greater size and robustness. He further recognized a size gradation through time, with the older *S. c. megalopeza* being the largest and *S. c. intermedia* intermediate in size between the former species and modern *S. cunicularia.*

Speotyto cunicularia intermedia is known only by a tarsometatarsus, and it is not comparable to the Inglis specimens. Only the coracoid (UF 30170) from Inglis 1A can be compared to two specimens referred to *S. c. megalopeza* (UMMP 27147 and 27152). UF 30170 measures least breadth and depth of the shaft, 2.6 and 2.1; sternal breadth and depth, 7.9 and 2.2. UMMP 27147 measures least breadth and depth, 2.7 and 2.1; sternal breadth and depth, 9.2 and 2.7. UMMP 27152 measures least breadth and depth, 2.6 and 2.1; sternal breadth and depth, 8.2 and 2.3. These measurements indicate that the Inglis specimen is slightly smaller than *S. c. megalopeza* and larger than the living species. As further size comparisons are not possible at this time, the Inglis material is referred only to species.

Discussion.—This material represents the earliest record of the Burrowing Owl in eastern North America; it also has been reported from the late Pleistocene of Reddick and Haile 11B, Florida (Brodkorb 1957; Ligon 1965). This species currently is resident in open prairies in central Florida (Stevenson and Anderson 1994).

Strix varia Barton 1799

Referred material.—Lecanto 2A: distal left tarsometatarsus, UF 101508.

Inglis 1A: right humerus with proximal end damaged, UF 30174; right carpometacarpus, UF 30175.

Discussion.—The material from Inglis 1A represents the earliest fossil occurrence of *Strix varia.*

Asio sp.

Referred material.—Inglis 1A: left coracoid missing head, UF 30178; distal right humerus, UF 30179; distal right tibiotarsus, UF 30180.

Measurements.—UF 30179 measures distal breadth and depth, 13.6 and 6.6; least breadth and depth of shaft, 5.7 and 4.8. UF 30180 measures distal breadth and depth, 9.4 and 7.6.

Description.—This material is within the size range of modern *Asio flammeus,* but is too fragmentary for specific identification. Two fossil species of *Asio* are known: *A. priscus* from the late Pleistocene of Santa Rosa Island, California (Howard 1964b; Guthrie 1992), and *A. brevipes* from the late Pliocene of Idaho (Ford and Murray 1967). Of these *A. priscus* is known by a complete tibiotarsus that is larger than UF 30180 (see measurements in Howard 1964b) and with an internal condyle that is higher posteriorly relative to its depth than in *A. flammeus, A. otus,* and UF 30180. *Asio brevipes* is known only by a distal tarsometatarsus and is not comparable with the material from Inglis 1A.

Discussion.—Only one other specimen of the genus *Asio* has been reported from the late Pliocene of North America, a scapula (UMMP 31892) from Fox Canyon, Kansas (Ford 1966). This specimen also could not be referred to species and is similar in size to *A. flammeus* and *A. otus* (Ford 1966).

Aegolius acadicus (Gmelin 1788)

Referred material.—Lecanto 2A: left tarsometatarsus missing proximal end, UF 101501 (Fig. 13).

Measurements.—UF 101501 measures least breadth and depth of shaft, 3.2 and 2.1; distal breadth, 6.8 mm; middle trochlea breadth and depth, 2.4 and 3.2.

Description.—The specimen compares well in size and characters to modern *Aegolius acadicus,* especially in its narrower proximal and distal breadths compared to *A. funereus* (Fig. 13; see table 5 in Emslie 1985 for measurements of modern *A. acadicus* and *A. funereus*).

Discussion.—UF 101501 is the first fossil record of *Aegolius acadicus* in Florida. The Northern Saw-whet Owl is a casual fall and winter visitor in northeastern Florida today (Stevenson and Anderson 1994). Its presence at Lecanto 2A suggests a coniferous forest habitat in this region during the late Pleistocene, the preferred environment of the living species (de la Torre 1990).

Strigidae, indeterminate

Referred material.—Lecanto 2A: pedal phalanx, UF 128750.

FIG. 15. Anconal view of left humerus missing distal end (UF 159397) of *Ceryle torquata* from Haile 7C, Florida. Scale 1×; bar = 1 cm.

Order CORACIIFORMES
Family ALCEDINIDAE

Ceryle torquata (Linnaeus 1766)

Referred material.—Haile 7C: left humerus missing distal end, UF 159397 (Fig. 15).

Measurements.—UF 159397 measures proximal breadth and depth, 12.9 and 4.8; least breadth and depth of shaft, 4.7 and 4.0.

Description.—This specimen compares well in size and characters to females of this species (*n* = 4♂, 4♀, USNM). In anconal view, the bicipital crest joins the shaft farther distally in *Ceryle torquata* than in UF 159397.

Discussion.—Fossils of kingfishers are rare. This specimen is the earliest record *Ceryle torquata* for North America, and the first record of the Ringed Kingfisher in the eastern USA. The species occurs in Mexico and the southwestern USA today, as well as throughout tropical regions of South America (AOU 1983).

Order PICIFORMES
Family PICIDAE

Melanerpes cf. *M. erythrocephalus* (Linnaeus 1758)

Referred material.—Inglis 1C: four distal mandibular symphyses, UF 165508, 165512, 165572, 165604.

Description.—These specimens compare well in size and characters to this species; *Melanerpes carolinus* has a narrower bill and *M. formicivorus* has a shallower symphysis than *M. erythrocephalus.*

Melanerpes sp. Swainson 1832

Referred material.—Cutler Hammock: distal right tarsometatarsus, UF 159104.

Haile 16A: distal right humerus, UF 102399.

Inglis 1A: humeral right coracoid, UF 30249; left coracoid, UF 30261; sternal right and left coracoids, UF 30250; right humerus, UF 30262; four proximal right humeri, UF 30242, 30263–30265; left humerus missing distal end, UF 30266; two distal left humeri, UF 30267, 30268; three proximal right ulnae, UF 30271–30273; two proximal left ulnae, UF 30269, 30270; two distal right ulnae, UF

30274, 30275; three distal left ulnae, UF 30276–30278; two distal left femora, UF 30246; proximal left tibiotarsus, UF 30279; left tarsometatarsus, UF 30280; two distal right tarsometatarsi, UF 30281, 30282; distal left tarsometatarsus, UF 30283; two shafts left tarsometatarsi, UF 30284, 30285.

Description.—These specimens compare well in size and features to both *Melanerpes carolinus* and *M. erythrocephalus.* However, these two species overlap in size and the fossil material cannot be reliably identified to either species. Only one element, UF 30280, closely matches *M. erythrocephalus* in size and characters and may be referable to that species.

Picoides cf. *P. villosus* (Linnaeus 1766)

Referred material.—Inglis 1A: proximal left tarsometatarsus, UF 30241.

Inglis 1C: distal mandibular symphysis, UF 165573; left tarsometatarsus, UF 165616; distal left tarsometatarsus, UF 165615.

Description.—These specimens are similar in size and characters to *Picoides villosus,* particularly in the shaft and features of the distal trochleae of the tarsometatarsus that serve to distinguish this genus from *Sphyrapicus* (narrower shaft and more expanded distal end) and *Melanerpes* (larger internal trochlea). *Picoides borealis* and *P. pubescens* are slightly smaller than *P. villosus* and the fossil material.

Discussion.—These specimens are the first records of *Picoides villosus* from Florida, and the earliest from North America. The Hairy Woodpecker also has been reported from the late Pleistocene of California (Miller and de May 1942) and Alabama (Parmalee 1992).

Colaptes auratus (Linnaeus 1758)

Referred material.—Cutler Hammock: proximal right scapula, UF 159223.

Haile 16A: distal left tarsometatarsus, UF 31925.

Inglis 1A: proximal right scapula, UF 30251; left coracoid, UF 30252; anterior carina of sternum, UF 30253; shaft left humerus, UF 30254; proximal left ulna, UF 30255; three distal right ulnae, UF 30256–30258; distal left tibiotarsus, UF 30260; shaft right tarsometatarsus, UF 30259.

Dryocopus sp.

Referred material.—Cutler Hammock: distal left ulna, UF 102285; distal right carpometacarpus, UF 102286.

Inglis 1A: distal right humerus, UF 30240.

Description.—These specimens compare well in size and characters to *Dryocopus pileatus,* but can not be reliably distinguished from *D. lineatus.*

Picidae, indeterminate

Referred material.—Inglis 1A: humeral right coracoid, UF 30248; humeral left coracoid, UF 30247; proximal right humerus, UF 30243; two distal left ulnae, UF 30244; distal left radius, UF 30245; medial fragment of pelvis, UF 30239.

Inglis 1C: three distal mandibular symphyses, UF 165502, 165505, 165549; distal left tarsometatarsus missing trochleae, UF 165613.

Order PASSERIFORMES

Family CORVIDAE

Cyanocitta cristata (Linnaeus 1758)

Referred material.—Inglis 1A: proximal left mandible, UF 31489.

Description.—This specimen compares well in size and characters to the living species.

Discussion.—This specimen is the earliest fossil record of *Cyanocitta cristata* in North America. The Blue Jay also has been reported from the late Pleistocene of Reddick 1A and Arredondo 2A, Florida, and Virginia and Missouri (Parmalee 1972; Brodkorb 1978).

Aphelocoma coerulescens (Bosc 1795)

Referred material.—Inglis 1A: two premaxillae, UF 31436, 31449; proximal right mandible, UF 31483; proximal left mandible, UF 31486; five distal mandibles, UF 31451, 31460, 31461, 31468, 31472; three left humeri, UF 31644–31646.

Description.—These specimens are discussed in detail by Emslie (1996). Except for a slightly shorter bill, they compare well with the modern Florida Scrub-jay, *Aphelocoma coerulescens coerulescens.*

Pica pica (Linnaeus 1758)

Referred material.—Lecanto 2A: proximal left mandible, UF 101530.

Reddick 1A: two left coracoids, UF/PB 968, 1372; humeral right coracoid, UF/PB 5038; two right scapulae, UF/PB 4595, 4797; left scapula, UF/PB 3736; right humerus, UF/PB 6814; two distal right humeri, UF/PB 839, 7650; left humerus, UF/PB 428; three distal left humeri, UF/PB 351, 832, 2765; left ulna, UF/PB 425; right carpometacarpus, UF/PB 1030; right femur, UF/PB 1387; two distal left tarsometatarsi, UF/PB 833, 1245.

Description.—The proximal mandible (UF 101530) is easily distinguished from other corvids by its size (larger than jays, smaller than *Corvus*) and by the absence of a prominent buttress that characterizes New World jays (Zusi 1987). It compares well in size and characters to *Pica pica.* In completing these comparisons, specimens referred to the extinct jay *Protocitta dixi* Brodkorb 1957 also were examined and found to fall within the size and range of variation of *Pica pica* (*n* = 5♀ and 2♂; FLMNH). In particular, characters of the humerus cited by Brodkorb (1957) in the generic diagnosis of *Protocitta dixi* do not differ significantly from *Pica pica,* especially in the size and shape of the internal tuberosity and angle of the medial bar. Other elements referred to the extinct species by Brodkorb (1957) and in the collections at FLMNH also were examined and found to compare well in size and characters to *Pica pica* except for UF/PB 425 and 1372, which were slightly larger than males of this species. Based on these comparisons, *Protocitta dixi* is hereby considered to be a synonymous with *Pica pica.*

A left humerus (UF 102272) tentatively referred to *Protocitta dixi* by Emslie and Morgan (1995) is considered to represent an indeterminate Icterinae (see below). Other elements from Haile 11B, Florida (Ligon 1965), referred to *Protocitta dixi* could not be located at FLMNH, although one specimen (UF 7206) from this site can be referred to cf. *Pica pica* (see below); specimens referred to

Protocitta dixi from Miller's Cave, Texas (Brodkorb 1978), were not examined, but are presumed to represent *Pica pica* pending additional study.

Discussion.—These specimens represent the first record of the Black-billed Magpie in Florida. The species also has been reported from the late Pleistocene of Alabama, Virginia, Tennessee, and Georgia (Parmalee 1992), and the early Pleistocene of Texas (Miller and Bowman 1956). The presence of the Black-billed Magpie in Florida supports Parmalee's (1992) conclusion that this species probably was once widespread in its distribution in eastern North America. Magpies occupy forested and riparian regions in western North America today and their presence at five localities in Florida (see below) suggests that similar habitats existed near these sites during the late Pleistocene.

cf. *Pica pica* (Linnaeus 1758)

Referred material.—Cutler Hammock: humeral right coracoid, UF 159386; left humerus, UF 102272; distal left humerus, UF 159308; two distal left ulnae, UF 159300, 159301; proximal left carpometacarpus, UF 159349; proximal right femur, UF 102271; distal right tibiotarsus, UF 159331; distal left tibiotarsus, UF 102276.

Haile 11B: distal left tibiotarsus, UF 7206.

Description.—These elements compare well in size and characters to *Pica pica,* but are too fragmentary for precise identification.

Discussion.—These specimens represent the most southern record of *Pica pica* in the eastern USA. In completing these comparisons, a distal left humerus (UF 16705) from Coleman 2A referred to the extinct jay, *Protocitta ajax,* by Ritchie (1980) was examined; it also appears to represent *Pica pica* and is tentatively referred to this species.

Corvus cf. *C. brachyrhynchos* Brehm 1822

Referred material.—Cutler Hammock: humeral left coracoid, UF 159389; distal left femur, UF 102253; distal right tibiotarsus, UF 159329; distal left tibiotarsus, UF 159328; distal right tarsometatarsus, UF 159375; proximal left tarsometatarsus, UF 159272; two distal left tarsometatarsi, UF 159372, 159373.

Haile 16A: left femur, UF 102397.

Corvus ossifragus Wilson 1812

Referred material.—Cutler Hammock: proximal left scapula, UF 159268; right coracoid, UF 159383; humeral right coracoid, UF 159387; three left humeral coracoids, UF 102255, 102265, 159388; two proximal right humeri, UF 102257, 159222; proximal left humerus, UF 159111; two distal right humeri, UF 102259, 159314; three distal left humeri, UF 102258, 159310, 159311; three proximal right ulnae, UF 102277, 159182, 159286; six proximal left ulnae, UF 159279–159283, 159285; seven distal right ulnae, UF 159290–159293, 159295–159297; six distal left ulnae, UF 102262, 102264, 102268, 159298, 159299, 159302; four proximal right carpometacarpi, UF 102260, 159360–159362; seven proximal left carpometacarpi, UF 102263, 159348, 159350–159354; four distal right carpometacarpi, UF 159363–159366; three distal left carpometacarpi, UF 102254, 159367, 159368; six proximal right femora, UF 159341–159346; two proximal left femora, UF 159337, 159340; two distal right femora, UF 159206, 159347;

two distal left femora, UF 159176, 159263; four distal right tibiotarsi, UF 102269, 159330, 159332, 159333; five distal left tibiotarsi, UF 102256, 159323, 159325–159327; four proximal left tarsometatarsi, UF 102261, 159103, 159317, 159369; two proximal right tarsometatarsi, UF 102266, 159371; distal right tarsometatarsus, UF 102267; distal left tarsometatarsus, UF 159102.

Inglis 1A: left humerus missing proximal end, UF 31643; left ulna, UF 31508; proximal left tibiotarsus, UF 31607; distal right tibiotarsus, UF 31640; distal left tibiotarsus, UF 31637.

Discussion.—The material from Inglis 1A represented the oldest fossil occurrence of *Corvus ossifragus,* which is common throughout Florida today (Stevenson and Anderson 1994).

Corvus sp.

Referred material.—Haile 7C: distal half left tarsometatarsus, UF 159399.

Measurements.—UF 159399 measures least breadth and depth of shaft, 3.4 and 2.7; distal breadth, 6.3; breadth and depth of middle trochlea, 2.4 and 4.1.

Description.—UF 159399 represents a crow that is smaller than females of *Corvus brachyrhynchos* and larger than *C. ossifragus.* The specimen approaches the size of *C. jamaicensis, C. palmarum,* and *C. nasicus,* but differs by a more robust middle trochlea than found in these three species. UF 159399 also was compared to *C. leucognaphalus* and *C. cryptoleucus*; these species are larger than UF 159399 and have a larger metatarsal facet. *Corvus imparatus* is smaller than UF 159399 with a more deeply excavated metatarsal facet.

The fossil species *Corvus neomexicanus* is known from the late Pleistocene of New Mexico (Magish and Harris 1976) and Utah (Emslie and Heaton 1987). This species, considered to be synonymous with *C. corax anticorax* by Brodkorb (1978), is intermediate in size between *C. cryptoleucus* and *C. corax,* and is larger than UF 159399. *Corvus wetmorei* from the late Pleistocene of New Providence Island, Bahamas (Brodkorb 1959), is considered by Olson and Hilgartner (1982) to be synonymous with *C. nasicus. Corvus pumilis* from the late Pleistocene and Holocene of Puerto Rico and St. Croix (Wetmore 1920) also is considered to represent either the living *C. nasicus* or *C. palmarum* (Olson and Hilgartner 1982). *Corvus galushai* is known by a left carpometacarpus from the late Miocene–early Pliocene Big Sandy Formation, Arizona, and is similar in size to *C. imparatus* (Bickart 1990).

Discussion.—This specimen probably represents an undescribed species of *Corvus,* but additional material is needed for adequate diagnosis and description.

Corvidae, indeterminate

Referred material.—Cutler Hammock: two proximal right ulnae, UF 102273, 102275; proximal left ulna, UF 102274; distal right ulna, UF 102270.

Family MUSCICAPIDAE
Subfamily TURDINAE

Catharus sp. Bonaparte 1850

Referred material.—Inglis 1C: partial premaxilla, UF 165552.

Description.—UF 165552 compares well in size and features to *Catharus gut-*

tatus, C. ustulatus, and *C. fuscescens,* but is too fragmentary for specific identification.

cf. *Hylocichla mustelina* (Gmelin 1789)

Referred material.—Inglis 1A: partial premaxilla, UF 31450; matching proximal right and left mandibles, UF 31480, 31481.

Description.—These specimens were compared to *Turdus, Sialia, Myadestes, Catharus, Hylocichla,* and *Turdus.* They compare most closely to *Hylocichla mustelina* (4♂, USNM) in characters, but are slightly larger and more robust than this species.

Discussion.—This tentative record would be the first and earliest for this species in North America.

Turdus sp. A

Referred material.—Inglis 1A: partial premaxilla, UF 165571; two distal mandibular symphyses, UF 165629, 165630.

Inglis 1C: partial premaxilla, UF 165625; five distal mandibular symphyses, UF 165501, 165507, 165514, 165515, 165550.

Description.—These specimens are from a robin larger than *Turdus migratorius.* They compare most closely to *T. rufiventris* and *T. rufopalliatus* in size and characters, but are too fragmentary for specific identification.

Turdus sp. B

Referred material.—Inglis 1C: three partial premaxillae, UF 165609, 165610, 165614; distal mandibular symphysis, UF 165503.

Description.—Except for UF 165503, the specimens are slightly smaller than *T. migratorius* and compare most closely to *T. plebejus* and *T. ignobilis.* UF 165503 is most similar to *T. migratorius* in size and characters.

Turdinae, indeterminate

Referred material.—Inglis 1C: distal mandibular symphysis, UF 165504.

Description.—The specimen compares most closely to *Turdus* in morphology except for the presence of a distinct ridge on the ventral midline.

Discussion.—This specimen, along with *Turdus* sp. A, *Turdus* sp. B, and cf. *Hylocichla mustelina* reported above, indicates that at least four species of thrush were present in the Florida peninsula in the late Pliocene. Two of these species may represent living taxa found today in arid regions of Mexico and Central America.

Family MIMIDAE

Dumetella carolinensis (Linnaeus 1766)

Referred material.—Inglis 1C: premaxilla, UF 165522.

Description.—This specimen compares well in size and characters to the living species.

Discussion.—This is the first fossil record of *Dumetella carolinensis* in Florida. The species also has been reported from the late Pleistocene of Alabama (Parmalee 1992).

Toxostoma rufum (Linnaeus 1758)

Referred material.—Inglis 1C: partial premaxilla, UF 165612.

Description.—UF 165612 compares well in size, shape, and morphology of ventral midline groove and dorsal foramina with modern specimens of *Toxostoma rufum. Dumetella carolinensis* and *Mimus* spp. are smaller, and other species of *Toxostoma* have premaxillae curved downward, unlike the condition in the fossil specimen, which is straight.

Discussion.—This specimen represents the earliest fossil record of *Toxostoma rufum.* The presence of two mimids at Inglis 1C suggest a habitat of thick brush and deciduous forest or hammock at the site during the late Pliocene, contrasting with the more open habitat represented at Inglis 1A.

Family EMBERIZIDAE

Vermivora cf. *V. celata* (Say 1823)

Referred material.—Inglis 1A: premaxilla, UF 31434.

Description.—The specimen also is similar to the premaxilla of *Vermivora pinus,* but most closely matches the size and features in *V. celata* and is tentatively referred to that species.

Discussion.—This is the first record of *Vermivora celata* from Florida and the earliest from North America. The Orange-crowned Warbler currently is a winter resident in Florida (Stevenson and Anderson 1994).

Cardinalis cardinalis (Linnaeus 1758)

Referred material.—Cutler Hammock: distal mandible, UF 159376.

Haile 16A: distal mandible, UF 31970.

Inglis 1A: distal mandible, UF 31476.

Inglis 1C: two premaxillae, UF 165598, 165599; distal mandibular symphysis, UF 165593.

Description.—The distal mandible of this species is distinguished from those of *Pitylus, Caryothraustes, Pheucticus,* and *Guiraca* by the angle, breadth, and depth of the distal symphysis.

Discussion.—The material from Inglis 1A and 1C represents the oldest fossil record of *Cardinalis cardinalis,* a common resident throughout Florida today (Stevenson and Anderson 1994).

cf. *Passerina* sp.

Referred material.—Haile 16A: distal mandible, UF 31973.

Description.—This specimen represents a bunting similar to *Passerina amoena, P. cyanea,* or *P. ciris,* but it is too fragmentary for positive identification.

Cardinalinae, indeterminate

Referred material.—Haile 16A: proximal right mandible, UF 159466.

Inglis 1C: partial mandible, UF 165510.

Description.—These specimens were compared to *Cardinalis, Guiraca, Pheucticus, Pitylus,* and *Caryothraustes.* UF 159466 did not match any of these genera in characteristics of the proximal mandible. It may represent an undescribed genus of grosbeak, but additional specimens are needed for adequate diagnosis and description. UF 165510 compares most closely to *Guiraca caerulea,* but it is too fragmentary for positive identification.

Spizella cf. *S. pusilla* (Wilson 1810)

Referred material.—Inglis 1C: premaxilla, UF 165517; four distal mandibular symphyses, UF 165602, 165603, 165607, 165622.

Description.—These specimens compare well in size and proportions to *Spizella pusilla,* which has a narrower or shorter symphysis than in *S. arborea, S. passerina,* and *S. pallida,* and a longer and broader symphysis than in *S. breweri.*

Discussion.—The Field Sparrow also has been reported from the late Pleistocene of Arredondo 2A, Florida (Brodkorb 1959).

cf. *Chondestes grammacus* (Say 1823)

Referred material.—Inglis 1C: distal mandibular symphysis, UF 165513.

Description.—This specimen compares well in morphology and size to *Chondestes grammacus,* but also is similar to *Pooecetes gramineus.*

Discussion.—This would be the first fossil record for Florida and the earliest in North America for *Chondestes grammacus,* which also has been reported from the late Pleistocene of Rancho La Brea, California (Dawson 1948).

Passerculus sandwichensis (Gmelin 1789)

Referred material.—Haile 16A: proximal left mandible, UF 159473; distal mandible, UF 31974.

Inglis 1A: three premaxillae, UF 31437, 31439, 31443; mandible missing left side, UF 31478; proximal right mandible, UF 31492; two proximal left mandibles, UF 31482, 31485; six distal mandibles, UF 31452, 31454, 31455, 31459, 31462, 31466.

Inglis 1C: premaxilla, UF 165518; proximal left mandible, UF 165519.

Description.—Because the mandible and premaxilla of *Passerculus sandwichensis* are most similar in size and morphology to those among the various species of *Ammodramus,* the fossil specimens were compared also to *A. savannarum, A. henslowii, A. leconteii, A. caudacutus, A. humeralis,* and *A. maritimus.* Of these, the bill of *A. savannarum* is similar in length to UF 31437, 31439, and 31443, but it is more robust than in *Passerculus sandwichensis* and has a small notch on the internal rim of the distal mandibular symphysis that is absent in this latter species. The bills of *A. henslowii, A. caudacutus,* and *A. humeralis* are slightly larger and more robust than that of *P. sandwichensis,* whereas that of *A. maritimus* is longer and less robust. The bill of *A. leconteii* is similar in size to the fossils and *P. sandwichensis,* but it is slightly less robust. UF 165518 has a slightly narrower bill and nasal bar and UF 165519 is more robust than females of *P. sandwichensis,* but both fossil specimens compare more closely to this latter species in size and other features than to other taxa listed above (see also characters of *Ammodramus* premaxillae given by Steadman 1981).

Discussion.—The material from Inglis 1A and 1C is the oldest fossil occurrence of *Passerculus sandwichensis.* The Savannah Sparrow also has been reported from the late Pleistocene Arredondo 2A (Brodkorb 1978) and Haile 11B (Ligon 1965), and is a common winter migrant in Florida today (Stevenson and Anderson 1994).

Ammodramus maritimus (Wilson 1811)

Referred material.—Inglis 1A: distal mandible, UF 31457.

Description.—This specimen is longer and more slender than the mandible of other species of *Ammodramus* (see description under *Passerculus sandwichensis* above) and compares best in size and proportions to *A. maritimus pelonota.*

Discussion.—This specimen is the first fossil record of *Ammodramus maritimus.* The Seaside Sparrow is a common breeding bird in coastal marshes on both coasts of Florida today (Stevenson and Anderson 1994). The subspecies *Ammodramus maritimus pelonota* occurs only on the northeastern coast in the state (Stevenson and Anderson 1994).

cf. *Passerella* sp.

Referred material.—Haile 16A: proximal right mandible, UF 159471; proximal left mandible, UF 159472.

Description.—These specimens are from a large, robust sparrow, larger than *Zonotrichia melodia* and near *Passerella iliaca* in size and features. They are too fragmentary for precise generic or specific identification.

Melospiza melodia (Wilson 1810)

Referred material.—Haile 16A: proximal left mandible, UF 159468.

Inglis 1A: proximal left mandible, UF 31488.

Description.—These specimens also were compared to *Passerella iliaca, Melospiza lincolnii, M. georgiana,* and *Zonotrichia leucophrys* and compare most closely in size and features to *M. melodia.* The mandible of *P. iliaca* is larger and more robust, whereas those of *M. lincolnii, M. georgiana,* and *Z. leucophrys* are smaller and more slender than that of *M. melodia* and the fossil material.

Discussion.—The fossil from Inglis 1A is the oldest occurrence of *Melospiza melodia*; both specimens are the first to be reported from Florida. The Song Sparrow is a common winter migrant in north Florida today (Stevenson and Anderson 1994).

Melospiza georgiana (Latham 1790)

Referred material.—Lecanto 2A: premaxilla, UF 101482.

Description.—This specimen also was compared to *Passerella iliaca, Melospiza lincolnii,* and *M. melodia* and most closely matches *M. georgiana* in relative size of the bill and nasal bar and size and depth of the ventral surface.

Discussion.—This specimen is the first fossil record of this species in Florida. The Swamp Sparrow is a regular winter migrant to north Florida today (Stevenson and Anderson 1994).

Zonotrichea cf. *Z. albicollis* (Gmelin 1789)

Referred material.—Inglis 1C: distal mandibular symphysis, UF 165619.

Description.—The specimen is slightly longer and larger than *Zonotrichea leucophrys* and compares well in size and features to *Z. albicollis.*

Zonotrichia cf. *Z. leucophrys* (Forster 1772)

Referred material.—Haile 16A: five premaxillae, UF 31977, 31978, 31980, 31981, 31987; distal mandible, UF 31976.

Inglis 1A: two distal mandibles, UF 31453, 31456.

Inglis 1C: four distal mandibles, UF 165505, 165506, 165516, 165555.

Description.—These specimens also were compared to *Zonotrichia albicollis* and *Z. atricapilla* and were found to most closely match *Z. leucophrys* in size and characters. However, similarity in characters among these three species allows only tentative identification.

Discussion.—The specimens from Inglis 1A and 1C, along with that of *Zonotrichia* cf. *Z. albicollis* reported above, would be the earliest records of these species in North America and the first fossil occurrences in Florida. The White-crowned Sparrow currently is a common winter migrant in Florida, although formerly it was uncommon to rare (Stevenson and Anderson 1994). These fossil records suggest that the species may have been common in the state during the late Pliocene and early Pleistocene as well.

Zonotrichia sp. Swainson 1832

Referred material.—Inglis 1A: partial premaxilla, UF 31444; distal mandible, UF 31469.

Description.—These specimens are too fragmentary for specific identification, but they are similar in size and features to *Zonotrichia albicollis, Z. atricapilla,* or *Z. leucophrys.*

Junco hyemalis (Linnaeus 1758)

Referred material.—Lecanto 2A: two premaxillae, UF 101483, 101509.

Haile 16A: two premaxillae, UF 31984, 31986; proximal right mandible, UF 159469; two proximal left mandibles, UF 159464, 159470; two distal mandibles, UF 31972, 31975.

Inglis 1C: premaxilla, UF 165617.

Description.—These specimens compare well in size and characters to the living species.

Discussion.—These specimens are the first records of *Junco hyemalis* from Florida and the earliest from North America. The Dark-eyed Junco is a common winter migrant in north Florida today (Stevenson and Anderson 1994).

Junco cf. *J. hyemalis*

Referred material.—Inglis 1A: premaxilla, UF 165570.

Inglis 1C: premaxilla, UF 165520.

Description.—These specimens compare well with *Junco hyemalis* in size and characters, except for the shape of the nares, which are not as elongated in UF 165570 and 165520 and have a straighter posterior border.

Agelaius phoeniceus (Linnaeus 1766)

Referred material.—Haile 16A: premaxilla, UF 31985; distal mandible, UF 105797.

Inglis 1A: mandible missing right proximal end, UF 31475.

Description.—These specimens are identical in size and characters to the living species.

Discussion.—*Agelaius phoeniceus* also was tentatively identified from Macasphalt Shell Pit (Emslie 1992) and is known from several late Pleistocene localities in Florida (Brodkorb 1978). The Red-winged Blackbird currently is a common resident throughout Florida (Stevenson and Anderson 1994).

cf. *Agelaius* sp.

Referred material.—Haile 7C: distal mandible, UF 159398.

Description.—This specimen is too fragmentary for specific identification, but appears most similar to *Agelaius* in size and characters.

Sturnella magna (Linnaeus 1758)

Referred material.—Inglis 1A: three premaxillae, UF 31441, 31446, 31470; proximal right mandible, UF 156788; proximal left mandible, UF 31487.

Description.—These specimens are slightly larger and more robust than *Sturnella neglecta* and compare well with *S. magna* in size and characters.

Discussion.—This species also has been reported from the late Pleistocene Eichelberger Cave, Arredondo 2A, and Haile 11B localities in Florida (Brodkorb 1956b, 1959; Ligon 1965). It is a common resident throughout the state today (Stevenson and Anderson 1994).

Euphagus cyanocephalus (Wagler 1829)

Referred material.—Inglis 1A: two premaxillae, UF 31442, 31448.

Description.—These specimens also were compared to *Euphagus carolinus* and found to most closely match *E. cyanocephalus* in size and proportions. One fossil species, *E. magnirostris,* also is known from the late Pleistocene of California (Miller 1929) and Wyoming (Emslie 1985). This species is distinguished by a shorter, more robust premaxilla compared to *E. cyanocephalus* and *E. carolinus.*

Discussion.—This is the first fossil record of *Euphagus cyanocephalus* from the eastern USA. Brewer's Blackbird also has been reported from late Pleistocene sites in Oregon, California, and Kansas (Brodkorb 1978). The species currently is a rare to common winter resident in Florida, and it is considered to have only recently extended its range into the state (Stevenson and Anderson 1994).

Euphagus sp.

Referred material.—Inglis 1A: partial premaxilla, UF 31435; proximal right mandible, UF 31484; distal mandible, UF 31458.

Description.—These specimens are slightly shorter and more robust than premaxillae of *Euphagus carolinus* and *E. cyanocephalus.* They may represent the extinct species *E. magnirostris,* known from the late Pleistocene of Rancho la Brea, California, and Little Box Elder Cave, Wyoming (Miller 1929; Emslie 1985), but they are too fragmentary for positive identification.

Quiscalus mexicanus (Gmelin 1788)

Referred material.—Lecanto 2A: left humerus, UF 101481.

Measurements.—UF 101481 measures length, 36.7; proximal breadth and depth, 9.9 and 3.6; least breadth and depth of shaft, 3.1 and 2.7; distal breadth and depth, 8.1 and 4.3.

Description.—UF 101481 compares well in size and proportions to females of *Quiscalus mexicanus,* especially to USNM 499280. Specimens of *Q. major, Q.*

quiscula, and *Q. niger* also were examined at USNM; males of all these species are larger, and females smaller, than *Q. mexicanus* and UF 101481.

Discussion.—This specimen represents the first record of *Quiscalus mexicanus* from Florida. The species currently is resident in the western USA and east to Arkansas and Louisiana (AOU 1983). UF 101481 is the first fossil record of Great-tailed Grackle and indicates the species had a more widespread distribution in the late Pleistocene than it does today.

Molothrus ater (Boddaert 1783)

Referred material.—Haile 16A: distal mandible, UF 31971.

Inglis 1A: two distal mandibles, UF 31471, 31473.

Description.—These specimens also were compared to *Molothrus aeneus* and found to match most closely the size and features of *M. ater.*

Discussion.—*Molothrus ater* also has been reported from the late Pleistocene of Reddick 1A (Hamon 1964) and Haile 11B (Ligon 1965). The Brown-headed Cowbird is a common resident throughout Florida today, having increased in numbers since it was first recorded as a breeding bird in 1957 (Stevenson and Anderson 1994).

Emberizinae, indeterminate

Referred material.—Inglis 1C: four distal mandibular symphyses, UF 165509, 165601, 165620, 165621.

Description.—These specimens are recognizable as a small sparrow, but are too fragmentary for identification.

Icterinae, indeterminate

Referred material.—Cutler Hammock: left humerus missing distal end, UF 102272.

Lecanto 2A: two right humeri, UF 101529, 128749; proximal right humerus, UF 101526; distal left humerus, UF 101528.

Haile 16A: proximal right mandible, UF 159465.

Passeriformes, indeterminate

Referred material.—Cutler Hammock: 40+ postcranial elements.

Lecanto 2A: right coracoid, UF 101521; humeral right coracoid, UF 128769; sternal right coracoid, UF 128768; two left humeri, UF 101525, 101527; left ulna, UF 101523; proximal right radius, UF 101516; left carpometacarpus, UF 101524; two right femora, UF 101517, 101518; two left femora, UF 101519, 101520; proximal right tibiotarsus, UF 128775; distal right tibiotarsus, UF 128776; left tarsometatarsus, UF 101513.

Haile 16A: medial fragment of left mandible, UF 159467; 100+ postcranial elements.

Inglis 1A: hundreds of catalogued and uncatalogued specimens (complete and fragmentary) representing all major postcranial elements.

Inglis 1C: four distal mandibular symphyses, UF 165511, 165606, 165611, 165618; right coracoid, UF 165579; right humerus missing proximal end, UF 165565; distal right humerus, UF 165585; left humerus missing proximal end, UF 165548; right ulna, UF 165556; right carpometacarpus, UF 165547; left femur, UF 165553; right tarsometatarsus, UF 165576; left tarsometatarsus, UF 165580; distal left tarsometatarsus, UF 165587.

DISCUSSION

> *The intriguing problems of biogeography require for their solution the services of collectors, taxonomists, paleontologists, geologists, ecologists, archeologists, palynologists, climatologists, and others. If the present trend toward compartmentalization of knowledge be deemed inevitable, then let me end with a plea for interdiscipline cooperation.* (Neill 1957)

The extensive avifaunas identified and described above, in addition to previously published data, provide a remarkable record of fossil birds for the Plio–Pleistocene of Florida. This record allows analysis of avian extinctions, biogeography, and community change correlated with paleoecological conditions and climate change over the past 2.5 Ma. This period was particularly dynamic in Florida, where the peninsular geography and low topography allowed impacts from even minor changes in sea level to be magnified beyond those in other regions with higher topography. By integrating the avian fossil record with information from geology, palynology, and climatology, the data provide a compelling account of avifaunal community history in the Florida peninsula. The need for such integrated approaches to understand historical biogeography in Florida was recognized by Neill (1957), but now can be accomplished with greater precision because of GIS technology and advancements in understanding the geology and paleontology of Florida.

ESTABLISHING AN AVIAN CHRONOLOGY

The first step in completing an analysis of Plio–Pleistocene avian originations and extinctions relative to climate change in Florida is to establish a chronology of all known taxa from the peninsula as provided by the fossil record. Using data presented here, in combination with that already available in the literature, and with certain modifications discussed above, an avian chronology for the Plio–Pleistocene of the Florida peninsula is presented in Table 14. This chronology includes 239 taxa, of which 60 (25.1%) are extinct. Some of these latter taxa remain undescribed, and are referred to genus or family only, primarily because of inadequate fossil material.

Several biases and potential problems with the chronology presented in Table 14 are inherent in the fossil data. First, the chronology is limited by the relative age of each fossil locality. These ages may be estimated within a comparatively brief or long interval of time, and the inability to obtain paleomagnetic, radiocarbon, or uranium-series dates precludes precise correlation of many originations and extinctions with specific climatic events. In addition, the fossil record can never be complete and many origins and extinctions for taxa are biased by this incomplete record. For example, the late Pliocene (2.5–2.0 Ma) of Florida is characterized by high originations of primarily aquatic birds. This bias can be attributed to the poor fossil record in Florida for the early Pliocene that, if better known, might extend the origination of some taxa to this earlier period, and to the absence of terrestrial avifaunas prior to the latest Pliocene Inglis faunas. In addition, the late Pleistocene record is biased in being the best represented period with at least 23 sites and 150 avian taxa in the chronology, 72 (48%) of which

TABLE 14. Stratigraphic distribution of extinct (denoted by dagger†) and extant birds in the late Pliocene to late Pleistocene of Florida. A plus sign (+) on the left side of the stratigraphic range indicates those taxa that have a fossil record in Florida and/or the eastern U.S. that extends earlier than that shown here; double plus signs (++) on the left or right side of the stratigraphic range indicate taxa with a fossil record in the western U.S, that extends earlier and/or later, respectively, than that shown for Florida. Letters on the far right for extant Florida species indicate: B = breeds in the state, W = common to uncommon winter/spring resident or transient, R = rare, only one to a few records in the state; a pound sign (#) indicates extant taxa that no longer occur in Florida. Inferred general habitat requirements for each taxon are indicated by numbers: (1) dry thorn-scrub, grassland, or savannah, (2) subtropical forest and hammock, (3) continental pine and deciduous forests, (4) freshwater aquatic and semi-aquatic, (5) coastal and marine; multiple habitat designations are ordered with the primary habitat for each species given first (data on current status and habitat in Florida are from Stevenson and Anderson 1994).

TAXON		PLIOCENE \ PLEISTOCENE \ HOLOCENE	
Ma	3.0	2.0 1.0 0.01	
Gavia pacifica^{5}		---	R
Gavia immer^{5}		-----------------------------------	W
†*Gavia concinna*^{5}	+	-----------------	
Tachybaptus dominicus^{4}		------------	R
Podilymbus podiceps^{4}	+	--	B
Podiceps auritus^{5,4}		--------------	W
†*Podiceps* sp.^{4}		------------------	
Pelecanus cf. *P. erythrorhynchos*^{4,5}		----------------	W
Phalacrocorax auritus^{4,5}		-----------------------------------	B
Phalacrocorax sp. (small)^{4,5}		-------	
†*Phalacrocorax filyawi*^{5}		-----	
†*Phalacrocorax idahensis*^{4}	++	---	
Anhinga anhinga^{4}		-----------------------------------	B
†*Anhinga beckeri*^{4}		--------------------------	
Botaurus lentiginosus^{4}		--	W
†*Botaurus* sp. (small)^{4}		-----	
Ixobrychus exilis^{4}		--	B
Ardea herodias^{4}		------------------------------	B
Ardea alba^{4}		--	B
†*Ardea* sp. A (small)^{4}		-----	
†*Ardea* sp. B (large)^{4}		------	

TABLE 14. Continued.

TAXON	PLIOCENE		\ PLEISTOCENE	\	HOLOCENE
Ma	3.0	2.0	1.0	0.01	
Egretta thula[4, 5]				----------------	B
Egretta caerulea[4, 5]				----------------	B
Egretta cf. *E. tricolor*[5, 4]			--------------------------------	--------------------------------	B
Egretta sp.[4, 5]		-------------------	-------------------		
Butorides virescens[4]			--------------------------------	--------------------------------	B
†*Butorides validipes*[4]		------			
Nycticorax nycticorax[4]				----------------	B
Nyctanassa violacea[4, 5]		--	--	--	B
Eudocimus albus[4, 5]				----------------	B
Eudocimus albus or *E. ruber*[4, 5]		--	--	--	
†*Eudocimus leiseyi*[4, 5]		-------------------	-------------------		
Ajaia ajaja[4]				----------------	B
†*Ajaia chione*[5, 4]			-------		
Mycteria americana[4, 5]				----------------	B
†*Ciconia maltha*[4, 5]		----------------------------------	----------------------------------	----------------------------------	
†*Ciconia* sp. (small)[4, 5]	+		-------		
†*Teratornis merriami*[1, 4]			----------------------	----------------------	
†*Teratornis* cf. *T. incredibilis*[1, 4]			-------		
Coragyps atratus[1, 2]		--	--	--	B
Cathartes aura[1, 2, 3]				----------------	B
Gymnogyps californianus[1]				----	#
†*Gymnogyps kofordi*[1]			-------		
†cf. *Gymnogyps* sp.[1]		----------			
†*Aizenogyps toomeyae*[1]		---			
Phoenicopterus ruber[5, 4]			-------		W
Phoenicopterus sp.[5, 4]		------			
†*Phoenicopterus copei*[5, 4]			-------	++	
†*Phoenicopterus* sp. (small)[5, 4]		------			
Dendrocygna sp.[4]		------			
Cygnus columbianus[5, 4]				----------------	R
Cygnus buccinator[4]			----------------------	----------------------	#
Branta canadensis[4, 5]		--	--	--	W
†*Branta dickeyi*[4, 5]	++		-------	++	

TABLE 14. Continued.

TAXON	PLIOCENE		\ PLEISTOCENE	\	HOLOCENE
Ma	3.0	2.0	1.0	0.01	
†*Anabernicula gracilenta*[4,5]		------	------	++	
†*Anabernicula* cf. *A. minuscula*[4,5]	+ ++	------			
†*Helonetta brodkorbi*[4]		------			
Aix sponsa[4]		------	------	------	B
Anas crecca[4]		------	------	------	W
Anas rubripes[5,4]				------	W
Anas fulvigula[4,5]				------	B
Anas platyrhynchos[4]		------	------	------	W
Anas acuta[4,5]				------	W
Anas discors[4]		------	------	------	W
Anas cyanoptera[4]		------			W
Anas clypeata[4]		------	------	------	W
Anas strepera[4]				------	W
Anas americana[4,5]		------	------	------	W
Aythya valisineria[4,5]				------	W
Aythya americana[4,5]			------	------	W
Aythya collaris[4]			------	------	W
Aythya marila[5,4]			------	++	W
Aythya affinis[5,4]			------	------	W
Somateria spectabilis[5,4]			------		R
Clangula hyemalis[5,4]				------	W
Bucephala clangula[4,5]				------	W
Bucephala albeola[4,5]		------	------	------	W
†*Bucephala* sp.[4,5]			------		
Lophodytes cucullatus[4,5]			------	------	W
Mergus merganser[4,5]	++			------	R
Mergus serrator[5,4]			------	------	W
Oxyura jamaicensis[4]				------	W
†*Oxyura hulberti*[4]		------			
Pandion haliaetus[4,5]				------	B
Haliaeetus leucocephalus[4,5]				------	B
†*Neophrontops slaughteri*[1]	++	---			
Circus cyaneus[4,1]			------	++	W

TABLE 14. Continued.

TAXON	PLIOCENE \		PLEISTOCENE \		HOLOCENE
Ma	3.0	2.0	1.0	0.01	
Accipiter striatus[2,3]				------	W
Accipiter cooperii[2,3]		------	------	------	B
Buteogallus urubitinga[2]		---			#
†*Buteogallus fragilis*[2]		----		++	
Buteo lineatus[2,4]		------	------	------	B
Buteo platypterus[2,3]			------	------	B
Buteo jamaicensis[1,2,3]			------	------	B
Buteo lagopus[1]			------	------	R
†*Buteo* sp. (large)[1]		------	------		
†*Amplibuteo woodwardi*[2]			------	--- ++	
†*Amplibuteo* sp. A[2]		------	------		
†*Amplibuteo* sp. B[2]	++	---			
Aquila chrysaetos[1,3]			------	------	R
Aquila sp. A[1]		------	------		
†*Aquila* sp. B[1]	++	---			
†*Spizaetus grinnelli*[2]				--++	
†*Spizaetus* sp.[2]		-----			
Caracara plancus[1]				------	B
Milvago chimachima readei[1]				----	#
Falco sparverius[1,2,3]		------	------	------	B
Falco columbarius[1,2]		------	------	------	W
Falco peregrinus[1,2,4,5]				------	W
†Cracidae, indet.[1,2]		------	------		
Tympanuchus cupido[1]				----	#
Meleagris gallopavo[3,2]				------	B
†*Meleagris leopoldi* or *M. anza*[3,2]	++ --	------	------		
Meleagris sp.[3,2]		------	------	------	
Colinus virginianus[1,2]	------	------	------	------	B
†*Neortyx peninsularis*[1]				----	
Coturnicops noveboracensis[4]			------	------	W
Laterallus exilis[4]		------	------	------	#
Rallus elegans[4]			------	------	B
Rallus longirostris or *R. elegans*[4,5]	------	------	------	------	B

TABLE 14. Continued.

TAXON	PLIOCENE		\ PLEISTOCENE	\	HOLOCENE
Ma	3.0	2.0	1.0	0.01	
Rallus limicola[4]	------	------	------	------	W
†*Rallus* sp. A[4]	------	------			
†*Rallus* sp. B[4]	------				
Porzana carolina[4, 5]		------	------	------	W
Porphyrula martinica[4]			------	------	B
†*Porphyrula* sp.[4]	------				
Gallinula chloropus[4]			------	------	B
Gallinula sp.[4]	------				
Fulica americana[4]	------	------	------	------	B
Aramus guarauna[4]			------	------	B
Grus canadensis[4, 2]	------	------	------	------	B
Grus americana[4]		------	------	------	#
†*Grus* sp. (large)[4]		------			
†*Titanis walleri*[1]	------			++	
Vanellus chilensis[1]			----		#
Charadrius vociferus[4, 5, 1]			------	------	B
†*Himantopus* sp.[4, 5]	------				
Recurvirostra americana[5, 4]			------	------	W
†*Recurvirostra* sp.[5, 4]	------	------			
Jacana spinosa[4]			------	------	#
Tringa melanoleuca[4, 5]			------	------	W
Tringa flavipes[4, 5]			------	------	W
cf. *Tringa* sp.[4, 5]	------				
Catoptrophorus semipalmatus[5]		---		++	B
Actitis macularia[5, 4]	------	------	------	------	W
Numenius americanus[5, 1]			------	------	R
Limosa cf. *L. fedoa*[5, 4]		------		++	W
Calidris cf. *C. canutus*[5]	------				W
Calidris cf. *C. alba*[5, 4]	------			++	W
Calidris cf. *C. pusilla*[5, 4]			------	------	W
Limnodromus scolopaceus[4, 5]		------	------	------	W
Limnodromus sp.[4, 5]	------	------			
Gallinago gallinago[4]		------	------	------	W

TABLE 14. Continued.

TAXON	PLIOCENE		\ PLEISTOCENE	\	HOLOCENE
Ma	3.0	2.0	1.0	0.01	
†*Gallinago* sp. (small)[4]	------				
Scolopax minor[4,3]			------	------	B
†*Scolopax hutchensi*[4,3]	------	------			
Stercorarius sp.[5]	------				
†*Larus perpetuus*[5]	+ ------				
†*Larus lacus*[5]	------				
†Alcidae, indet.[5]		-------			
Columba fasciata[3,2]			----		#
Zenaida macroura[1,2]		------	------	------	B
cf. *Zenaida* sp.[1,2]			----		
†cf. *Ectopistes migratorius*[3,1]			------	------	W
Coccyzus americanus[2,3]		------	------	------	B
Tyto alba[2,1]		------	------	------	B
Otus asio[2,3]		------	------	------	B
Bubo virginianus[2,3]		------	------	------	B
†*Glaucidium explorator*[2,3]		---			
†*Glaucidium* sp.[2,3]		---			
Speotyto cunicularia[1]		------	------	------	B
Strix varia[3,2]		------	------	------	B
Asio flammeus[1,4]			------	------	W
Asio sp.[1,2,3]		---			
Aegolius acadicus[3]			----		R
Ceryle torquata[4,5]		---			#
Ceryle alcyon[4]			------	------	B
Melanerpes cf. *M. erythrocephalus*[3,2]		------	------	------	B
Melanerpes sp.[3,2]		------	------	------	B
Picoides cf. *P. villosus*[3,2]		---	++		B
Picoides borealis[3]			------	------	B
Colaptes auratus[3,2]		------	------	------	B
Dryocopus sp.[3,2]		------	------	------	B
Tyrannus tyrannus[3,2,1]			------	------	B
Progne subis[1,3,4]			------	------	B
†*Tachycineta speleodytes*[1,4]			----		
Cyanocitta cristata[3]		------	------	------	B

TABLE 14. Continued.

TAXON	PLIOCENE	\	PLEISTOCENE	\	HOLOCENE
Ma	3.0	2.0	1.0	0.01	
Aphelocoma coerulescens coerulescens[1]		----------	----------	----------	B
Pica pica[1, 3]				----	#
†*Protocitta* cf. *P. ajax*[2]	++		----		
†*Henocitta brokborbi*[2]				----	
Corvus brachyrhynchos[3, 2, 1]		------	----------	----------	B
Corvus ossifragus[5, 3]		----------	----------	----------	B
†*Corvus* sp.[3, 2, 1]		---			
Sitta pusilla[3]				---------------	B
Troglodytes aedon[1, 2, 3]				---------------	W
Cistothorus platensis[1, 4]				---------------	W
†*Cistothorus brevis*[1, 4]				----	
Sialia sialis[3, 1]				---------------	B
Catharus minimus[3]				---------------	W
cf. *Hylocichla mustelina*[3, 2]		---			B
Turdus sp. A[2, 3]		---			
Turdus sp. B[2, 3]		---			
Dumetella carolinensis[1, 2, 3]		---			B
Mimus polyglottos[1, 2]				---------------	B
Toxostoma rufum[3, 1]		----------	----------	----------	B
Lanius ludovicianus[1, 3]				---------------	B
Vireo griseus[3, 2]				---------------	B
Vermivora cf. *V. celata*[3, 2]		---			W
Dendroica sp.[3, 2]			----		
Geothlypis trichas[4, 3]				---------------	B
Cardinalis cardinalis[3, 1]		----------	----------	----------	B
Pheucticus ludovicianus[3]			----	---------------	W
cf. *Passerina* sp.[3]		-------			
Cardinalinae, indet.[3]		------------			
Pipilo erythrophthalmus[3, 2]			----	---------------	B
Aimophila aestivalis[3]			----	---------------	B
Spizella passerina[3, 1]				---------------	W
Spizella pusilla[1]			----	---------------	W
Pooecetes gramineus[1]			----	---------------	W

TABLE 14. Continued.

TAXON	PLIOCENE		\ PLEISTOCENE		\ HOLOCENE
Ma	3.0	2.0	1.0	0.01	
cf. *Chondestes grammacus*[1]		---			W
Passerculus sandwichensis[1]		---	---	---	W
Ammodramus savannarum[1]				---	W
Ammodramus henslowii[1,3]				---	W
Ammodramus maritimus[5]		---			B
cf. *Passerella* sp.[3]		---	---		
Melospiza melodia[4]		---	---	++	W
Melospiza georgiana[4,5]				---	W
Zonotrichia cf. *Z. albicollis*[3,1]		---			W
Zonotrichia cf. *Z. leucophrys*[1,3]		---	---	++	W
Junco hyemalis[3]		---	---	---	W
†*Cremaster tytthus*[2]				---	
†*Pandanaris floridana*[2]				---	
Dolichonyx oryzivorus[1]				---	W
Agelaius phoeniceus[4,1]	---	---	---	---	B
cf. *Agelaius* sp.[4,1]		---			
Sturnella magna[1]		---	---	---	B
Euphagus cyanocephalus[1]		---		++	W
Euphagus sp.[1]		---			
Quiscalus mexicanus[1,2,4]				---	#
Quiscalus major[5,4]				---	B
Quiscalus quiscula[3,1]				---	B
Molothrus ater[3,1]		---	---	---	B

appear as fossils for the first time in Florida. Only two sites represent the period 1.0–0.3 Ma, with a combined species richness of 38 taxa. As a result of these biases, species richness varies significantly from an even distribution among the five time periods represented ($\chi^2 = 46.8$, df = 4; $P < 0.005$). These problems hinder a precise analysis of patterns in avian originations and extinctions with climate change. Nevertheless, this chronology provides a record for birds unmatched from any other region of the world and a working model that can be revised with future additions to the fossil record.

BIOGEOGRAPHY OF EXTANT TAXA IN THE PLIO–PLEISTOCENE

The chronology indicates that of the 162 extant species represented in the fossil record, 77 (47.5%) currently are breeding birds in the Florida peninsula, 64 (39.5%) are winter–spring residents or transients, and 21 (13%) are rare or do not occur in Florida today. Many of the winter–spring residents or transients are waterfowl and passerines and the fossil data suggest that current migratory patterns for these species were established in the late Pliocene. Passerines in this category include one warbler (*Vermivora* cf. *V. celata*) and 12 sparrows (Table 14), all of which currently breed in northern continental habitats. It also is possible that during glacial stages, the breeding range of these species extended into the Florida peninsula as did their habitats, or that their habitat preferences were broader in the past. Palynological evidence for the late Pleistocene, for example, indicates the extension of northern coniferous forests (including spruce [*Picea*]) into the Florida panhandle from 14,000 to 12,000 before present (BP) (Watts et al. 1992; Watts and Hansen 1994), and broad-leaved, mesic forest into the north Florida peninsula from 15,000 to 12,000 BP (Watts and Hansen 1988). Moreover, spruce pollen is present in the sediments from Inglis 1A (F. Rich, pers. comm.), a site also presumed to date to a glacial stage (Morgan and Hulbert 1995), but in the late Pliocene. If similar responses by plant communities during glaciations in the late Pleistocene are assumed to have occurred in earlier glaciations, then further evidence for northern coniferous forests in the late Pliocene in the Florida peninsula is to be expected.

Extant taxa in the chronology that are rare or absent from Florida today include primarily species of western North America or those with southern, Neotropical affiliations. Several species are found today in subtropical to tropical wetlands (*Tachybaptus dominicus, Laterallus exilis, Jacana spinosa, Ceryle torquata*), forests (*Buteogallus urubitinga*), or grasslands (*Milvago chimachima, Vanellus chilensis*). The remaining taxa largely occur in western prairies, grasslands, and chaparral (*Gymnogyps californianus, Aquila chrysaetos, Buteo lagopus, Tympanuchus cupido, Quiscalus mexicanus*), western wetlands and coastal habitats (*Gavia pacifica, Cygnus columbianus, C. buccinator, Somateria spectabilis, Mergus merganser, Grus americana, Numenius americanus*), or northern forest (*Aegolius acadicus, Columba fasciata*). Many of these species probably were able to extend their ranges into the Florida peninsula with the development of the Gulf Coast corridor during glacial stages (see below). Other taxa in the chronology, primarily waterfowl, may have had a more extensive range (especially in winter) that included the peninsula because of loss of suitable habitat in the north as a result of glacial advances.

The avian chronology also is notable for its absences, especially of Neotropical migrants including warblers. This absence may be a factor of the fossil record, but extensive avifaunas that include dozens of identified passerine premaxillae and mandibles from Inglis 1A and Reddick 1A suggest otherwise (although hundreds of postcranial bones from these sites cannot be identified to species). Based on this negative evidence, it is possible to suggest, albeit cautiously, that current migratory patterns of most Neotropical warblers and other migrants did not develop in the peninsula until the early Holocene, after the retreat of the last major glaciation. Because most modern, North American forest communities did not appear until the early Holocene, these migratory species may not have developed their current breeding ranges until these communities became established (see also Williams and Webb 1996).

AVIAN COMMUNITY, CLIMATE, AND SEA-LEVEL CHANGES

Since the discovery of oxygen isotope ratios as proxy indicators of past temperatures and sea levels, knowledge of past cycles of global climate change has increased substantially (see Dawson 1992 for a summary). Recent studies indicate that climatic shifts follow 40,000-, 23,000-, 11,000-, and 6,100-years or shorter cycles in correlation with Milankovitch and Heinrich events and variations in solar activity (Dwyer et al. 1995; Kerr 1996). These studies also allow correlation of vertebrate evolution and extinction with climatic events (Monastersky 1996; Potts 1996). Investigations of ostracods and other invertebrates in fossil marine deposits, ancient shorelines, and raised beaches have been especially important in studies on sea-level and climatic change in the Gulf of Mexico, the Florida peninsula, and the Atlantic coastal plain (MacNeil 1950; Pirkle et al. 1970; Blackwelder et al. 1979; Cronin 1980, 1983; Cronin et al. 1981; Bloom 1983; Krantz 1991). Results from these and other investigations are used here to model sea-level history of the Florida peninsula with data from Plio–Pleistocene fossil localities.

The impact that sea-level change has had on the Florida peninsula is especially dramatic, because of its low topography and the shallow continental shelf in the Gulf of Mexico. Using GIS maps of the peninsula (Figs. 16, 17), it is possible to calculate relative land area lost or gained with sea-level change from present conditions (Table 15). These data indicate that more land area is lost with sea-level rise than is gained with sea-level regression, especially within the first 10 m of change. For example, a rise of 10 m from present sea level would decrease the land area of the peninsula by 53.3%, but if sea level was lowered by 10 m, only half that area (25.7%) is gained (Table 15). The difference between land area lost or gained decreases with changes above 10 m, and becomes slightly greater for area gained with changes at 40 m and above. Thus, minor fluctuations in sea level from present conditions will affect land area more so with marine transgressions than with regressions. This impact is especially important to consider with current global warming, the measured rise in sea level of 3.9 mm/yr (Nerem 1995), and the potential effect of this rise on coastal and terrestrial communities in the Florida peninsula.

Investigations of current sea-level change and its impact on coastal wetlands also indicate relatively rapid ecosystem response to minor fluctuations. Coastal marshes in New England and the Gulf of Mexico have shown significant decline and turnover in dominant vegetation over the past 50 yr in direct response to local sea-level rise at 2.0–2.5 mm/yr (Warren and Niering 1993). These vegetational changes occurred in part from a slight increase in tidal flooding and peat salinity caused by rising sea level and reflect the delicate balance that these ecosystems maintain at the margins of terrestrial and marine environments. Similar rapid changes have been documented for the replacement of freshwater marshes by salt marshes in California (Davis 1992), the expansion of coastal marshes at 1,000-ka intervals during the Holocene in the northeastern USA (Rampino and Sanders 1981), and for the variable location of archaeological sites on coastal South Carolina (Colquhoun et al. 1981). From these data, it is not unreasonable

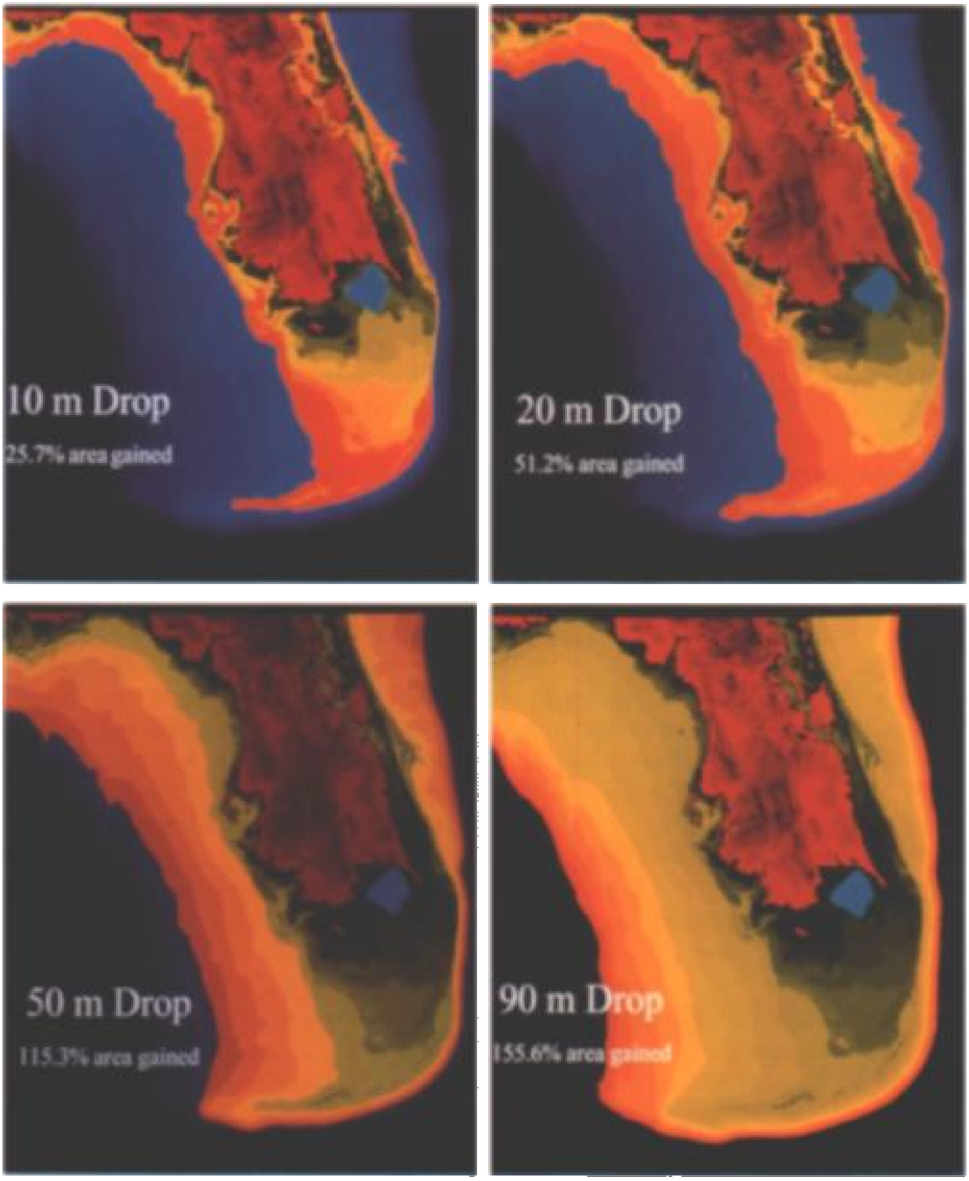

FIG. 16. Geographic Information Systems (GIS) maps of Florida at increasingly lower sea levels than today (top left to bottom right). Increases in land area of the peninsula, especially with the emergence of the shallow continental shelf in the Gulf of Mexico, allowed development of the Gulf Coast corridor that extended around the Gulf and along the eastern margin of Mexico and Central America. A 90-m drop (lower right) is approximately equivalent to that experienced in the last glaciation (Wisconsinan) in the late Pleistocene.

to hypothesize that sea-level fluctuations in the past have had a significant influence on coastal and terrestrial communities in the Florida peninsula, especially when glacial and interglacial stages occurred relatively frequently (at least 21 glacial cycles since 2.3 Ma have been documented by the oxygen isotope record

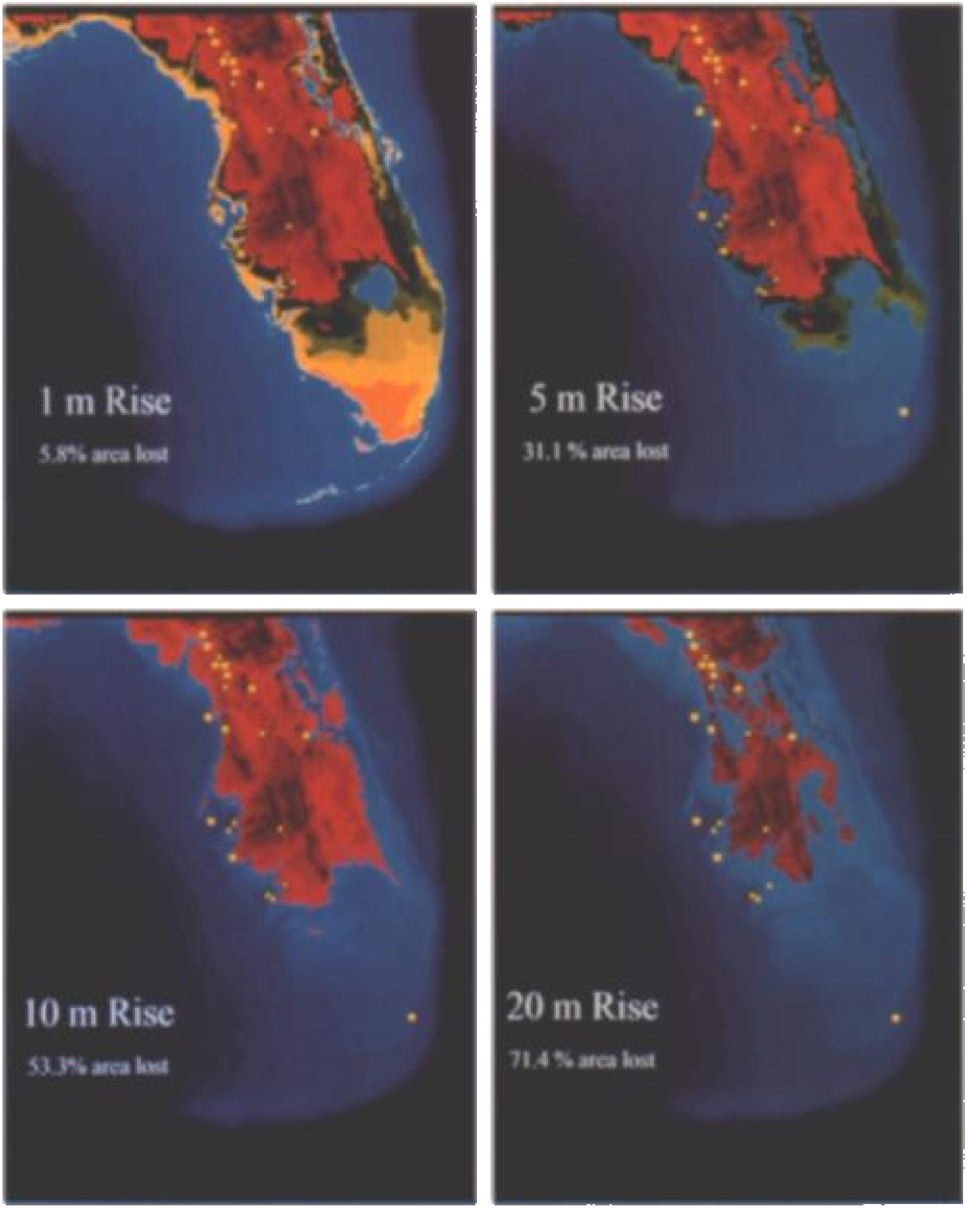

FIG. 17. Geographic Information Systems (GIS) maps of Florida at higher sea levels than today (top left to bottom right) with locations (yellow symbols) of major fossil localities discussed in the text (see Fig. 1 for site names and explanation of symbols). Only a relatively small rise in sea level (5 m; upper right) would submerge south Florida and the extensive wetlands that exist there today.

in marine sediments; van Donk 1976) and rapidly (within 10^4–10^5 yr for the last interglacial; Cronin 1987).

Published estimates of sea-level change in the Plio–Pleistocene of Florida and the Atlantic coastal plain are summarized in Table 16. The estimates are imprecise because of variations in the data upon which they are based (Cronin et al. 1981; Krantz 1991) and because of the confounding effects of tectonic and epeirogenic

TABLE 15. Cumulative and percent change in hectares (ha) of land area gained or lost with sea-level fluctuations in the Florida peninsula. The cumulative area gained or lost was calculated from modern sea level for that portion of the peninsula shown in Figures 16 and 17, using 30°N latitude as the northern boundary.

Sea-level fall/rise (m)	Land area gained/lost (ha)	Cumulative land area gained/lost	
		Hectares	%
−100	+696,755	+17,890,262	161.9
−90	+826,797	+17,193,507	155.6
−80	+901,781	+16,366,710	148.1
−70	+1,356,655	+15,464,929	140.0
−60	+1,375,782	+14,108,274	127.7
−50	+1,698,156	+12,732,492	115.3
−40	+2,263,251	+11,034,336	99.9
−30	+3,109,970	+8,771,085	79.4
−20	+2,820,103	+5,661,115	51.2
−10	+2,841,012	+2,841,012	25.7
+1	−640,898	−640,898	5.8
+2	−700,159	−1,341,057	12.1
+3	−598,256	−1,939,313	17.6
+4	−615,787	−2,555,100	23.1
+5	−700,519	−3,433,669	31.1
+6	−442,325	−3,875,994	35.1
+7	−629,645	−4,505,639	40.8
+8	−589,603	−5,095,242	46.1
+9	−463,135	−5,558,377	50.3
+10	−327,960	−5,886,337	53.3
+20	−1,997,561	−7,883,898	71.4
+30	−1,587,271	−9,471,169	85.7
+40	−1,060,330	−10,531,499	95.3
+50	−416,933	−10,948,432	99.1

TABLE 16. Estimated major sea-level changes from modern conditions during the Plio–Pleistocene as shown by studies specific to the Gulf of Mexico and the Atlantic coastal plain based on the oxygen isotope record and other data.

Age (Ma)	Oxygen isotope state	Sea level (m)	References
2.4	100	−85 to −25	Krantz 1991
2.2	87	+15	Krantz 1991
2.0	82	−75 to −10	Krantz 1991
1.88	75	<+15	Krantz 1991
1.64	63	<+15	Krantz 1991
1.6	62	−100 to −15	Krantz 1991
0.22	7	−12 to −32	Cronin et al. 1981
0.188	6	+12 to +2	Cronin et al. 1981
0.12	5e	+9 to +6	Cronin et al. 1981
0.105	5c	−15 to −13	Cronin et al. 1981
0.094		+3 to +10	Cronin et al. 1981
0.082	5a	−15 to −13	Cronin et al. 1981
0.072		+4 to +10	Cronin et al. 1981
0.018	2	−80 to −60	Blackwelder et al. 1979; Bloom 1983

uplift that occurred in Florida and the Atlantic coastal plain during the Pleistocene (Cronin 1980; Opdyke et al. 1984). Thus, land-area changes in the Florida peninsula associated with the estimated sea-level changes also are imprecise. However, the relative impact that these changes had on the peninsula and on avian communities, based on the fossil record, can be addressed to discern patterns in origins and extinctions associated with climate and sea-level changes in the Plio–Pleistocene. In addition, other global estimates of sea-level change (e.g., Haq et al. 1987) do not correspond entirely with those for the Atlantic coastal plain. Here, I consider the localized estimates to be most reliable for correlations to the avian record.

Prior to the initiation of the ice ages at about 2.5 Ma, there was a long period of high sea level and relative climatic stability in the early and early late Pliocene. Sea levels may have been as high as 80 m above current levels (Dwyer et al. 1995), and much of the Central American Isthmus was submerged causing North and South America to be isolated from each other. At 3.5–3.0 Ma and again at about 2.4 Ma, global cooling and glaciation caused a lowering of sea level to the extent that the Central American Isthmus emerged and formed a land bridge between the continents (Coates et al. 1992; Willard et al. 1993; Cronin and Dowsett 1996). This emergence had two major consequences to biological communities: a shift in ocean circulation that caused a lowering in productivity and turnover in marine molluscan and vertebrate faunas (Marshall et al. 1982; Stanley 1986; Coates et al. 1992; Jackson et al. 1993; Emslie and Morgan 1994; Petuch 1995; Allmon et al. 1996a, b), and the initiation on land of the Great American Biotic Interchange (Stehli and Webb 1985). It has been postulated that this interchange was facilitated by a broad expanse of savannah and thorn-scrub habitat, the Gulf Coast corridor, that developed with the emergence of the shallow continental shelf extending around the eastern border of Mexico to Texas and southeast to the Florida peninsula (but with some tropical forest barriers in the isthmus region, see Colinvaux 1993, 1996). Both events had a profound influence on marine and terrestrial communities that are well documented for invertebrates and mammals (Marshall et al. 1982; Stehli and Webb 1985; Allmon et al. 1993, 1996a, b; Jackson et al. 1993; Vermeij 1993; Vrba 1993; Willard et al. 1993). Data presented here now permit quantification and discussion of the avian record during the period from 2.5 to 0.01 Ma; these data are summarized in Table 17.

The late Pliocene.—Fossil avifaunas that date from 2.5 to 2.0 Ma are dominated by aquatic taxa. One of the richest localities, Macasphalt Shell Pit, probably formed in a freshwater marsh as reflected by the vertebrate fauna (Morgan and Ridgway 1987; Emslie 1992). This site, located 8 km east of the Gulf Coast, apparently formed when sea level was near that of today (Hulbert 1987; Morgan and Ridgway 1987), whereas 2 km east of Macasphalt Shell Pit the Richardson Road Shell Pit (Fig. 1) is characterized by a coastal depositional environment and must have formed at a slightly higher sea level than today (Emslie et al. 1996). This latter site also is the type locality for an extinct, presumably marine species of cormorant (*Phalacrocorax filyawi*) and it has produced the youngest record of an extinct seal (*Callophoca obscura*) in Florida (Emslie and Morgan 1994; Emslie 1995b). Both of these species disappeared from the Gulf of Mexico with other taxa affiliated with a cold-water, upwelling marine environment with the emergence of the isthmus and concomitant changes in ocean circulation and produc-

TABLE 17. Summary of avian origins and extinctions by major time intervals and primary habitat represented by each taxon during the Plio–Pleistocene of Florida. The total species richness known for each time period also is given with the percent of originations and extinctions.*

	Time period (Ma)				
	2.5–2.0	2.0–1.6	1.6–1.0	1.0–0.3	0.3–0.01
Origins	54†	66	34†	17	69†
Habitat 1	3	18	5	6	21
Habitat 2	1	12	2	3	5
Habitat 3	1	16	4	4	12
Habitat 4	38	15	14	4	23
Habitat 5	11	5	9	0	8
Extinctions	22†	30	32†	3	21†
Habitat 1	0	10	6	0	11
Habitat 2	1	7	1	2	5
Habitat 3	0	5	3	0	2
Habitat 4	12	5	14	1	3
Habitat 5	9	3	8	0	0
Total species	56	100	103	88	150
% Originations	96.4	66	33	19.3	46
% Extinctions	39.3	30	31.1	3.4	14

* Habitat types: 1 = dry thorn-scrub, grassland, or savannah; 2 = subtropical forest and hammock; 3 = continental pine and deciduous forest; 4 = fresh water aquatic and semiaquatic; 5 = coastal and marine.

† Origins or extinctions vary significantly by habitat (χ^2, df = 4, $P < 0.05$).

tivity (Allmon 1992; Emslie and Morgan 1994; Morgan 1994; Allmon et al. 1996a).

It appears from this record that Richardson Road Shell Pit is perhaps slightly older than Macasphalt Shell Pit and was formed during a late Pliocene interglacial. This period of deposition is estimated to have occurred when sea level was approximately 8–9 m higher than it is today as indicated by GIS maps of sea-level transgression at 1-m intervals. At 9 m above present sea level, a barrier island appears on the GIS maps near the coast and in the same location as Richardson Road Shell Pit, supporting the hypothesis by Emslie et al. (1996) that shell and bone deposits formed at this site through multiple breaching episodes at a barrier island beach. Subsequent regression of sea level to 25–85 m below that of today (Table 16) probably was occurring during formation of the deposits at Macasphalt Shell Pit as a freshwater and brackish-water marsh. This site also produced some of the earliest records of South American taxa in North America that were involved in the Great American Interchange, including *Holmesina floridanus* and *Dasypus bellus* (Morgan and Ridgway 1987), indicating that the Gulf Coast corridor was well established by 2.4 Ma. Thus, the deposits at Macasphalt Shell Pit mark a glacial stage at the beginning of the Great American Interchange in the Florida peninsula shortly after the emergence of the Central American Isthmus.

After this period of sea-level regression in the late Pliocene, sea level rose again to a point above modern conditions as shown by the presence of shallow, marine shell-bed faunas above the fossil-bearing deposits at Macasphalt and Richardson Road Shell Pits (Allmon 1993; Emslie et al. 1996). These beds may have been deposited at about 2.2 Ma when sea level is estimated to have been up to 15 m higher than it is today (Table 16). In addition, the Wicomico shoreline that dates to the late Pliocene or early Pleistocene was formed after fossils were deposited at Haile 15A and indicates a sea-level transgression of up to 32–35 m (Webb 1990). The end of this period at 2.0 Ma is marked by the disappearance of 22 avian taxa from the chronology (39.3% of total avian species richness, Table 17), of which all but one represent freshwater aquatic or coastal–marine habitats. The single exception is an extinct tropical hawk-eagle (*Spizaetus* sp.) that is known only from Macasphalt Shell Pit and represents the earliest occurrence of this genus in North America. The genus does not occur in Florida again until the late Pleistocene when *Spizaetus grinnelli* appears in the Vero Beach and Cutler Hammock faunas (Becker 1985a; data presented herein).

Although the high origination rate of aquatic taxa at 2.5 Ma may be a result of biases in the fossil record, the large number of marsh and wading birds that disappeared by 2.0 Ma may be associated with climatic and sea-level change that occurred during this period. The transgression at 2.2 Ma may have submerged at least 60% of the present-day Florida peninsula, thereby causing a significant decline in terrestrial habitat (Table 15; Fig. 17). This decline especially would have affected south Florida and the extensive wetlands that may have existed there during periods of lower sea levels. The impact on avian wetland communities would have been twofold: direct loss of habitat from submergence, and decrease in remaining habitat area and the number of species that could be supported.

The chronology (Table 14) indicates that of the 21 aquatic taxa that disappeared between 2.5 and 2.0 Ma, one is the marine cormorant from Richardson Road Shell Pit, eight represent extant taxa with a poor fossil record in Florida, and nine are extinct taxa. Of the latter, seven had a body-size that was smaller to slightly smaller (based on measurements of skeletal elements) than extant congeners or closely related species, whereas two (*Porphyrula* sp. and *Himantopus* sp.) were slightly larger than their modern counterparts (Emslie 1992). The other three extinct taxa are gulls (*Larus lacus* and *L. perpetuus*) and a jaeger (*Stercorarius* sp.) that, as with the cormorant, may have disappeared with changing marine conditions at the end of the Pliocene (Emslie 1995b). The bias in extinctions toward taxa with relatively small body-size suggests that rising sea level and loss of wetland habitat may have affected these species more so than those with larger body-sizes. If the population size of all wetland taxa is assumed to have declined with loss of habitat, this bias in the fossil evidence supports the theoretical prediction by Pimm et al. (1988) that the risk of extinction is less for large-bodied species of birds at low population sizes.

The Latest Pliocene.—The latest Pliocene (2.0–1.6 Ma) avifaunas of Florida, unlike the late Pliocene assemblages, are not biased towards aquatic taxa and include many terrestrial species as well (Table 17). The rich collection from Inglis 1A, supplemented with smaller collections from Inglis 1C and Haile 7C, provide considerable information on terrestrial avian communities in Florida beginning at about 2.0 Ma. Other avifaunas that date to this period are smaller and more aquatic in composition than those from Inglis and Haile. These sites include shell pit deposits in south Florida at De Soto, Pelican Road, Forsberg, and D&M, but they are notable in recording the presence of several extinct taxa (e.g., *Gavia concinna, Eudocimus leiseyi, Buteogallus fragilis*). The avian communities represented during this period, as with mammalian faunas, consist of numerous taxa with Neotropical affinities as well as North American continental species with a more southerly and easterly extension of their ranges than their modern counterparts.

For example, the chronology indicates that of 66 taxa that originate between 2.0 and 1.6 Ma, at least 8 (12.1%; including *Tachybaptus dominicus, Buteogallus urubitinga, B. fragilis, Amplibuteo* sp., and *Ceryle torquata*) are affiliated with tropical to subtropical habitats, whereas 18 (27.3%; including, *Neophrontops slaughteri, Aquila* sp., *Glaucidium* sp., *Speotyto cunicularia,* and *Aphelocoma coerulescens*) can be associated with dry, thorn-scrub and savannah environments that presumably dominated the Gulf Coast corridor. Taxa of aquatic (e.g., *Phalacrocorax idahensis*) and wooded environments also are represented. The Gulf Coast corridor would have been as extensive at 2.0 Ma as it was at 2.4 Ma when sea level was 10–75 m lower than it is today (Tables 15, 16; Fig. 16). It appears that the development of the corridor again facilitated range expansions of plants, mammals, and birds from the Neotropics and western North America to the Florida peninsula. Moreover, it is clear that these taxa represented many habitats and that the corridor probably was composed of a mosaic of dry savannah with scattered lakes, wetlands, and hammocks (Emslie and Czaplewski, in press).

At the end of this period at 1.6 Ma, 30 extinctions (30% of total species richness) occur, but these are equally dispersed among habitat types. Most of these extinctions (22) affect species associated with terrestrial habitats, including subtropical forests or hammocks and the dry, thorn-scrub and savannah habitat of the Gulf Coast corridor (Table 17). These collective extinctions account for 73.3% of all those recorded by the end of this period and imply that these habitats were reduced considerably by climatic events. Notable species that disappear from the record at this time include an extinct cormorant (*Phalacrocorax idahensis*), an Old World vulture (*Neophrontops slaughteri*), and a hawk and two eagles (*Buteogallus fragilis, Amplibuteo* sp., *Aquila* sp.) also known from western North America, a large extinct condor (*Aizenogyps toomeyae*), a tropical hawk (*Buteogallus urubitinga*), the Ringed Kingfisher (*Ceryle torquata*), and the only large, flightless phorusrhacoid (*Titanis walleri*) known from North America (Table 14). Two pygmy-owls (*Glaucidium explorator* and *Glaucidium* sp.) also originate and disappear during this time period, and they reflect both western and tropical to subtropical affinities. Additional extinctions of passerines include an undescribed, extinct species of crow (*Corvus* sp.) and two thrushes (*Turdus* spp.) that may represent living tropical taxa. All of these species suggest that during glacial stages the Florida peninsula experienced greater habitat diversity and heterogeneity than today, allowing for greater avian diversity within feeding guilds (e.g., vultures and raptors) and within specific communities (e.g., subtropical hammocks and woodlands). Unlike the previous event at the end of the late Pliocene, no correlation is apparent between avian extinctions and body size at 1.6 Ma.

Two marine transgressions are known during this time, both raising sea level up to 15 m above present conditions (Table 16). These transgressions also are apparent from shell deposits of the Caloosahatchee Formation above the bone-bearing units at De Soto, Forsberg, D&M, and Pelican Road Shell Pits that probably formed at 1.88 Ma (Table 16; Morgan and Hulbert 1995). Using GIS maps, all these sites except De Soto would be submerged with a sea-level rise of only 3 m above present conditions; De Soto, however is not submerged until there is a rise of more than 10 m (Fig. 17). The sea-level rises at 1.88 and 1.64 Ma, as with similar transgressions earlier in the late Pliocene, would have submerged the Gulf Coast corridor and caused the loss of considerable terrestrial habitat (up to ca. 60%; Table 15) in the Florida peninsula. The submergence of the corridor also may have reduced habitat diversity and heterogeneity and would help account for the avian extinctions discussed above. Only three taxa disappear that are representative of coastal habitats (Table 14), but all are extant species (*Gavia pacifica, Catoptrophorus semipalmatus, Ammodramus maritimus*), of which two currently breed in Florida and their absence may be simply an artifact of the fossil record.

Early and middle Pleistocene.—The early Pleistocene (1.6–1.0 Ma) also is represented by both terrestrial and aquatic avifaunas, but the regional isotopic record is poorly known (Table 16). The global record for this period based on deep-sea marine sediments and isotopes indicates a continuation of considerable climatic oscillation (Shackleton and Opdyke 1973; van Donk 1976). The largest fossil avifaunas of this age from Florida are from Leisey Shell Pit (Emslie 1995a) and Haile 16A. These assemblages reflect the occurrence of a nearly equal number of originations and extinctions, with significant differences in numbers among habitats represented (Table 17).

Taxa with aquatic and coastal adaptations appear and disappear at a higher rate (22% of total species richness for both) than do terrestrial species during this period. Relatively few tropical taxa (including *Ajaia chione, Amplibuteo* sp., a cracid, *Laterallus exilis,* and *Phoenicopterus ruber*) originate, compared to the previous period, and this implies high sea levels and the absence of a Gulf Coast corridor. Interestingly, this period also is marked by a brief appearance of an undetermined species of alcid at Leisey Shell Pit, if the age of these specimens is correct and they are not reworked from earlier deposits below that in which they were found (Emslie 1995a). Alcids, diverse in the early Pliocene of Florida, disappeared by the late Pliocene with other marine taxa when marine productivity declined in the Gulf of Mexico, as mentioned above. The two specimens from Leisey Shell Pit are similar to the living *Cerorhinca monocerata* (Emslie 1995a) and possibly represent a species that entered the Gulf of Mexico from the Pacific or North Atlantic.

Entrance by alcids from the Pacific would have been possible if the Central American Isthmus had resubmerged during the early Pleistocene. However, submergence of the isthmus currently would require a rise in sea level of at least 34 m (Savin and Douglas 1985). There is no evidence that an early Pleistocene interglacial caused a rise of this magnitude, nor do paleooceanographic data indicate a drop in sea temperatures resulting from cold-water upwelling that would be expected with this submergence, as was the case in the early Pliocene (Willard et al. 1993; Cronin and Dowsett 1996). Isotopic data indicate that sea levels fluctuated to as high and higher than current conditions during the early Pleistocene (van Donk 1976). Marine ostracods in the southeastern USA suggest that these fluctuations ranged from 22 to 35 m above present sea level (Cronin 1980), although determination of more precise sea levels during this period is confounded by tectonic and epeirogenic uplift. The GIS analyses completed for this study indicate that Leisey Shell Pit would be submerged with only a 3-m rise in sea level above that of today (Fig. 17). Shell beds associated with and above the bone-bearing units at this site are found in the Bermont and Ft. Thompson Formations; the latter is 3-m thick with 2.8 m of quartz sand and soil above it (Hulbert and Morgan 1989). Thus, a sea-level rise of only 3–4 m could account for the formation of the upper shell bed above the Leisey 1A bone-bearing unit.

It is more likely that the alcid from Leisey 1A represents a taxon that extended its range southward from the North Atlantic, where alcids have been known since the Miocene (Olson 1985). Three other such occurrences are known from bones of the Great Auk (*Pinguinus impennis*) and Common Murre (*Uria aalge*), which appear in archaeological sites dated at about 3,000 BP and 1300 AD from the northeast coast of Florida near Summer Haven, St. Johns County (Brodkorb 1960). These occurrences correlate with cooler climates than today (Brodkorb 1960), and it is possible that an alcid extended its range from the North Atlantic into the Gulf of Mexico during a glacial stage as part of a similar response in the early Pleistocene.

Extinctions of wetland taxa at 1.0 Ma are significant (Table 17), but do not suggest a pattern similar to that of the late Pliocene in being biased towards species with small body-size. Instead, a nearly equal number of taxa that were slightly to greatly larger than their modern counterparts, as well as those that were smaller, became extinct. Large, extinct taxa include a heron (*Ardea* sp.), spoonbill (*Ajaia chione*), flamingo (*Phoenicopterus copei*), goose (*Branta dickeyi*), hawk (*Buteo* sp.), crane (*Grus* sp.), and woodcock (*Scolopax hutchensi*); small taxa include a loon (*Gavia concinna*), ibis (*Eudocimus leiseyi*), stork (*Ciconia* sp.), pygmy-goose (*Anabernicula gracilenta*), rail (*Rallus* sp. A), and avocet (*Recurvirostra* sp.). Of these species, three (*P. copei, B. dickeyi, Anabernicula gracilenta*) survived until the end of the Pleistocene in western North America, suggesting only extirpation from the Florida peninsula at 1.0 Ma. These extinctions resulted in a loss of species richness in peninsular wetland communities by the end of the Pleistocene.

The late early and middle Pleistocene (1.0–0.3 Ma) is the most poorly known period in the avian chronology. Only two sites, Coleman 2A and the McLeod Limerock Mine, have produced notable fossil collections from this period. Birds from these sites indicate that more than one half of the originations were of taxa associated with the Neotropics and Gulf Coast corridor (Table 17), suggesting that a glacial stage once again allowed species to extend their ranges into Florida. Two western taxa, *Buteo lagopus* and *Aquila chrysaetos,* appear at this time and both remain as rare winter residents in the peninsula (Table 14). Only three taxa disappear during this period and the poor fossil record precludes further interpretations.

The late Pleistocene.—By far the best known time period in the Florida peninsula is the late middle and late Pleistocene (0.3–0.01 Ma). At least three episodes of sea-level regression are recorded (Table 16), of which the last, the Wisconsinan glaciation at 0.021–0.018 Ma, was the most significant with a sea-level drop of 60–80 m, and perhaps up to 120 m (Fairbanks 1989), below present level. This drop would have increased the land area of the Florida peninsula by 127–148% or more (Table 15) and greatly expanded the Gulf Coast corridor (Fig. 16). Numerous fossil localities in Florida have produced large and small collections of fossil birds that probably were deposited during and shortly after this glacial maximum; the richest sites include Reddick 1A (Brodkorb 1957; Hamon 1964), Arredondo 2A (Brodkorb 1959), Ichetucknee River (McCoy 1963; Campbell 1980), Rock Springs (Woolfenden 1959), Haile 11B (Ligon 1965), and Cutler Hammock (Emslie and Morgan 1995 and data presented herein). Unfortunately, absolute dating of these sites is not possible because the fossil material is too leached of organic material for radiocarbon analysis.

At least 150 taxa are represented from these sites, of which nearly half (69 or 46%) originate and only 21 (14%) become extinct; both categories vary significantly by habitats represented (Table 17). The former category is dominated by species associated with dry, open habitats of the Gulf Coast corridor, reflecting again the range expansions to the peninsula that occurred from western North America and the Neotropics during glacial stages. The number of tropical to subtropical taxa that appear in the peninsula, however, is unusually low (nine taxa or 13% of origins; Table 17) given the magnitude of the marine regression that occurred in the Wisconsinan glaciation. Those taxa with tropical affinities include *Ajaia ajaja, Spizaetus grinnelli, Caracara plancus, Milvago chimachima, Jacana spinosa, Vanellus chilensis, Henocitta brodkorbi, Cremaster tytthus,* and *Pandanaris floridana*; western taxa include *Gymnogyps californianus, Pica pica,* and *Quiscalus mexicanus.* In addition, two taxa with more northerly distributions today (*Aegolius acadicus* and *Columba fasciata*) are reported for the first time in Florida at Lecanto 2A. Their presence at this site suggests that these deposits formed during the full glacial, when northern coniferous forests extended farther southward than today and into the Florida panhandle (see discussion above).

The end of this period, as in the latest Pliocene, was marked by the disappearance of species largely with Neotropical and western affinities (13 taxa or 61.9% of all extinctions; Table 14). These taxa include all those with tropical affinities listed above except for *Ajaia ajaja* and *Caracara plancus,* both of which still breed in Florida (Table 14). Taxa that currently have their center of distribution in western North America and also still occur in Florida are limited to *Speotyto cunicularia* and *Aphelocoma coerulescens* (Emslie 1996). Isolation of this latter species in the peninsula since the late Pliocene resulted in a speciation event, and the Florida Scrub-jay is now recognized as a separate species from western scrub-jays (AOU 1995). The late Pleistocene extinctions also had little influence on wetland or coastal species, of which only three disappear. These three species include a large, extinct anhinga (*Anhinga beckeri*) and a stork (*Ciconia maltha*). The third species, the Trumpeter Swan (*Cygnus buccinator*), survives in western North America. These data suggest that modern wetland communities were well established in the peninsula by the end of the Pleistocene, and that they have undergone little change since that time.

Late Pleistocene extinctions, as with those in the early Pleistocene, again indicate more loss of species diversity within feeding guilds and specific communities. These extinctions include a teratorn (*Teratornis merriami*), the California Condor (*Gymnogyps californianus*), a tropical eagle (*Amplibuteo woodwardi*) and hawk-eagle (*Spizaetus grinnelli*), the Yellow-headed Caracara (*Milvago chimachima*), and the Southern Lapwing (*Vanellus chilensis*). Except for the caracara and lapwing, these taxa also occurred in western North America in the late Pleistocene. Other taxa that disappeared from the peninsula include a number of passerines that reflect the greater habitat diversity and heterogeneity that existed at that time because of the Gulf Coast corridor. These species include the Black-billed Magpie (*Pica pica*), two extinct icterids (*Cremaster tytthus* and *Pandanaris floridana*), and the Great-tailed Grackle (*Quiscalus mexicanus*). Fragmentation and submergence of the corridor, and the mosaic of environments it contained, may have helped cause the isolation and extinction of many of these species at 0.01 Ma. At least four marine transgressions, ranging in height from 2 to 13 m above current sea level (Table 16), are known to have occurred during the middle and late Pleistocene as evidenced by ancient shorelines and other data (Cronin et al. 1981; Webb 1990), and would have submerged this corridor (Table 15; Fig. 17).

These late Pleistocene extinctions also were influenced by the extensive continental losses of mammalian megafauna that also occurred at that time. These losses included 33 genera in North America (Martin 1984), about which there has been much debate as to their cause (e.g., Martin and Klein 1984 and papers therein). Regardless of the cause, numerous scavenging birds disappeared at the same time, probably because of their dependency on the megafauna for food. Nine of 19 genera of birds that disappeared in North America in the late Pleistocene are vultures or raptors, including a condor (*Breagyps clarki*), teratorns (*Teratornis* and *Cathartornis*), Old World vultures (*Neogyps, Neophrontops*), and eagles (*Amplibuteo, Wetmoregyps*) (Steadman and Martin 1984). In addition, the California Condor (*Gymnogyps californianus*) became extirpated over most of its former range (except the Pacific coast) in North America by 0.01 Ma (Emslie 1987a). Thus, extinctions of some of these birds in Florida was also influenced by the loss of the mammalian megafauna as well as the disappearance of the Gulf Coast corridor.

CONCLUSIONS

Climatic and sea-level changes have had a major influence on avian extinctions and community development in the Florida peninsula since the beginning of the ice ages at 2.5 Ma. Because of its low topography and peninsular geography, even minor fluctuations in sea level had considerable effect on the area and composition of peninsular habitats. The numerous and relatively rapid glacial and interglacial stages alternately either increased exposure of the shallow continental shelf around the Gulf of Mexico, or increased the extent of shallow marine environments over the margins of the peninsula. In the former case, a Gulf Coast corridor formed and facilitated the range expansion of taxa from the Neotropics and western North America into the peninsula. This corridor apparently consisted largely of dry thorn-scrub and savannah, but also had a mosaic of habitats including wetlands and hammocks. Numerous taxa of birds, mammals, reptiles, and plants with western and southern affinities appear in the Florida peninsula during glacial stages when this corridor was present. The formation of this corridor also increased the size of the Florida peninsula during glacial stages, in some cases by 148% or more of its current size. The terrestrial habitats apparently became more diverse and heterogeneous, because of the influx of northern and southern vegetation types, allowing for greater species richness in specific communities and feeding guilds than is found in the peninsula today.

During interglacial stages, the Gulf Coast corridor was reduced or eliminated by marine transgressions, with subsequent habitat fragmentation in western North America, the Neotropics, and the peninsula. This fragmentation would have resulted in loss of habitat diversity and heterogeneity in the peninsula, and the extinction, extirpation, or isolation of avian taxa in terrestrial communities. These communities also were affected by the continental extinctions of mammalian megafauna that occurred in the late Pleistocene, especially the commensal scavenging and raptorial birds. Wetland and coastal avian communities were affected most by marine transgressions in the late Pliocene and early Pleistocene and suffered a gradual loss of species richness through time. Taxa with small body-size compared to modern counterparts especially were affected by the extinctions in the late Pliocene. Modern wetland communities appear to have developed in the peninsula by the late Pleistocene with little change in avian species richness occurring thereafter. Modern terrestrial communities, and perhaps Neotropical migratory patterns, apparently did not develop until the early Holocene after the last extinction event at 0.01 Ma. These differences in age for the development of modern wetland versus terrestrial communities also suggest that these communities have disparate rates of species turnover and evolution, even when located in the same geographic region and subject to the same climatic events.

The avian chronology presented here provides a model for avian origins and extinctions associated with climatic change over the past 2.5 Ma in the Florida peninsula. This model can be modified and improved with future additions to the fossil record and with the development of more accurate methods to date fossil localities and correlate them with climatic events. This research also stands as a tribute to Dr. Pierce Brodkorb, his students, dedicated amateur paleontologists, and the value of interdisciplinary investigations to address complex research questions. Additional morphological, paleontological, and paleoecological studies of fossil birds will continue to add to our knowledge of the role of climate change in avian community history, biogeography, and extinctions in the Florida peninsula.

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