LATE PLEISTOCENE BIRDS FROM KINGSTON SALTPETER CAVE, SOUTHERN APPALACHIAN MOUNTAINS, GEORGIA

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Kingston Saltpeter Cave, Bartow County, Georgia, has produced late Quaternary fossils of 38 taxa of birds. The presence of extinct species of mammals, and three radiocarbon dates on mammalian bone collagen ranging from approximately 15,000 to 12,000 Cal B.P., indicate a late Pleistocene age for this fauna, although a small portion of the fossils may be Holocene in age. The birds are dominated by forest or woodland species, especially the Ruffed Grouse (*Bonasa umbellus*) and Passenger Pigeon (*Ectopistes migratorius*). Species indicative of brushy or edge habitats, wetlands, and grasslands also are present. They include the Greater Prairie Chicken (*Tympanuchus cupido*, a grassland indicator) and Black-billed Magpie (*Pica pica*, characteristic of woody edges bordering grasslands). Both of these species reside today no closer than 1000+ km to the west (mainly northwest) of Georgia. An enigmatic owl, perhaps extinct and undescribed, is represented by two juvenile tarsometatarsi. The avifauna of Kingston Saltpeter Cave suggests that deciduous or mixed deciduous/coniferous forests and woodlands were the dominant habitats in the late Pleistocene of southernmost Appalachia, with wetlands and grasslands present as well.

Key Words: Georgia; late Pleistocene; southern Appalachians; Aves; extralocal species; faunal change

INTRODUCTION

Numerous late Pleistocene vertebrate faunas have been recovered from caves and other karst features of the Appalachian region (listed in Lundelius et al. 1983; Graham & Lundelius 1994; Webb et al. 2004). While mammalian fossils have received the most attention, many of the Appalachian fossil localities also include a rich component of birds. The two southernmost of these avifaunas are from Bartow County, Georgia — Ladds Quarry Cave (Wetmore 1967; Olson 1984) and the topic of this paper, Kingston Saltpeter Cave (Fig. 1). Along with the avifauna from Bell Cave in northwestern Alabama (Parmalee 1992), the late Pleistocene bird communities from southern Appalachia are now well enough known to provide useful paleoenvironmental information.

Vertebrate fossils were discovered and collected at Kingston Saltpeter Cave (hereafter KSC) in the 1970s by L. O. Blair, J. M. Sneed, and R. Wilson. As is the case for most Appalachian cave deposits, the stratigraphy of the KSC fossil deposit is poorly developed. For lack of any contrary evidence, I regard all KSC bird fossils as being from a late Pleistocene accumulation that lacks internal stratigraphy. Three radiocarbon (14C)

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dates have been determined from mammal bones at KSC. The first $(10,300 \pm 130 \text{ yr B.P.}; \text{Beta-}12771, \text{un-}$ corrected for ${}^{13}\text{C}/{}^{12}\text{C}$; = 12,850 - 11,350 Cal B.P.) is based on collagen from unidentified scrap mammal bone. This date does not have the quality control of the other two broadly overlapping ¹⁴C dates, which are (at 95% confidence) 15,660 - 14,430 Cal B.P. (Beta-153622; bone collagen of the extinct peccary Mylohyus nasutus) and 15,460 - 14,170 Cal B.P. (Beta-153623; bone collagen of the extant deer Odocoileus virginianus). Although it may be that some bird fossils from KSC are Holocene rather than late Pleistocene in age, there are no preservational differences among these specimens that would suggest major differences in their ages. Only through radiocarbon dating many more individual bones, identified to species, can the chronology of cave sites such as KSC be improved (Steadman et al. 1997; Stafford et al. 1999). For now it seems reasonable to regard the entire avifauna as late Pleistocene in age.

MATERIALS AND METHODS

Unless cited otherwise, distributions are based upon the following references: Lundelius et al. (1983), Emslie (1998), and Webb et al. (2004) for late Pleistocene birds of North America, American Ornithologists' Union [A.O.U.] (1998) for modern birds elsewhere in North

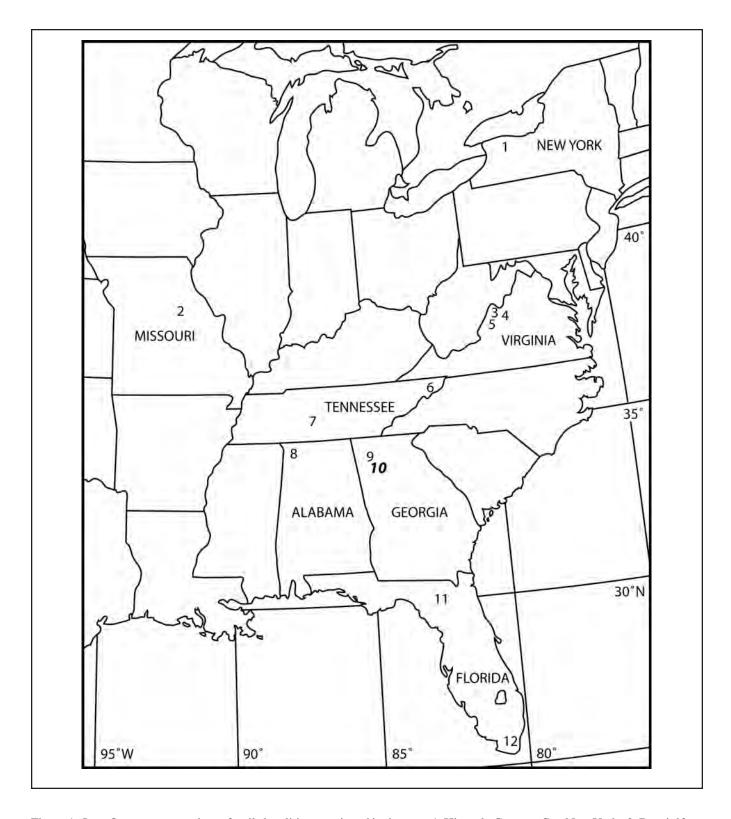


Figure 1. Late Quaternary vertebrate fossils localities mentioned in the text. 1, Hiscock, Genesee Co., New York. 2, Brynjulfson Cave II, Boone Co., Missouri. 3, Strait Canyon, Highland Co., Virginia. 4, Natural Chimneys, Augusta Co., Virginia. 5, Clark's Cave, Bath Co., Virginia. 6, Baker Bluff Cave, Sullivan Co., Tennessee. 7, Cheek Bend Cave, Maury Co., Tennessee. 8, Bell Cave, Colbert Co., Alabama. 9. Ladd's Quarry Cave, Bartow Co., Georgia. 10, Kingston Saltpeter Cave, Bartow Co., Georgia. 11, Ichetucknee River, Columbia Co., Florida. 12, Cutler Hammock, Dade Co., Florida.

America, and Burleigh (1958) and Beaton et al. (2003) for modern birds in the mountain province of northern Georgia. The higher level systematics, nomenclature, and sequence of species generally follow A.O.U. (1998). In the species accounts, the term "widespread" means a geographic range that spans at least 10° of latitude and 20° of longitude. The terms "the East" and "the West" are relative to the Mississippi River.

The KSC fossils are housed in the Vertebrate Paleontology Collection of the Frank M. McClung Museum, University of Tennessee, Knoxville. Modern bird skeletons used to identify the fossils are from the Florida Museum of Natural History (UF), New York State Museum (NYSM), and National Museum of Natural History, Smithsonian Institution (USNM). For extralocal species and selected species that are difficult to identify, osteological characters are presented under Remarks. Osteological nomenclature follows that of Howard (1929) and Baumel et al. (1993). Measurements are in mm, taken with digital calipers of 0.01 mm increments, rounded to the nearest 0.1 mm. In addition to the specimens listed in Table 1 and in the species accounts are 162 avian fossils from KSC that are either undiagnostic or that I did not attempt to identify, such as 119 vertebrae, many of which must belong to grouse.

SYSTEMATIC PALEONTOLOGY Order PODICIPEDIFORMES Family PODICIPEDIDAE

PODILYMBUS PODICEPS (Linnaeus) – Pied-billed Grebe

Material.—Quadrate, carpometacarpus, tarsometatarsus.

Late Pleistocene Status.—Widespread.

Modern Range in North America.—Widespread.

Modern Status in Northern Georgia.—Common migrant and winter visitor; breeds locally.

Order CICONIIFORMES

Family VULTURIDAE (CATHARTIDAE)

CORAGYPS ATRATUS (Bechstein) – Black Vulture Material.—Quadrate, mandible, humerus, ulna.

Late Pleistocene Status.—Widespread.

Modern Range in North America.—Absent from far north and west.

Modern Status in Northern Georgia.—Rare resident.

Remarks.—Each of the fossils is from a nestling bird, thereby demonstrating that *Coragyps atratus* once nested within or near KSC.

Order ANSERIFORMES Family ANATIDAE

ANAS cf. A. PLATYRHYNCHOS Linnaeus – probable Mallard

Material.—Furcula.

Late Pleistocene Status.—Widespread.

Modern Range in North America.—Widespread.

Modern Status in Northern Georgia.—Uncommon to common winter visitor.

ANAS DISCORS Linnaeus – Blue-winged Teal Material.—Furcula.

Late Pleistocene Status.—Widespread.

Modern Range in North America.—Widespread.

Modern Status in Northern Georgia.—Common migrant and winter visitor.

Remarks.—Skeletal elements of *Anas discors* can be difficult to distinguish from those of *A. crecca*, although males of *A. discors* are consistently larger than females of *A. crecca*. The furcula listed here agrees in size with that of a male *A. discors*. Similarly, the ulna and tarsometatarsus listed below for *A. crecca* agree in size with those of a female of that species.

ANAS CRECCA Linnaeus – Green-winged Teal

Material.—Ulna, tarsometatarsus.

Late Pleistocene Status.—Widespread.

Modern Range in North America.—Widespread.

Modern Status in Northern Georgia.—Uncommon migrant and winter visitor.

ANAS STREPERA Linnaeus - Gadwall

Material.—Tibiotarsus.

Late Pleistocene Status.—This is only the fourth North American record; the other record in the East is from Ichetucknee River, Florida.

Modern Range in North America.—Widespread but uncommon.

Modern Status in Northern Georgia.—Uncommon migrant and winter visitor.

Remarks.—Based on size, this specimen probably belonged to a male of *Anas strepera*. A femur from KSC, referred to *Anas* sp. (indeterminate dabbling duck), is approximately the size of a male *A. clypeata* or a female *A. strepera*, but is otherwise undiagnostic.

ANAS ACUTA Linnaeus - Pintail

Material.—2 tibiotarsi.

Late Pleistocene Status.—Common in western

Table 1. Birds from Kingston Saltpeter Cave, Bartow County, Georgia. NISP, number of identified specimens; MNI, minimum number of individuals represented by the identified specimens. Habitat preferences: A, aquatic; F, forest (closed canopy) or woodland (large trees, but with open canopy); G, grasslands; I, indeterminate; M, mixed wooded and non-wooded, forest edge, or brushy. *, species reported also from Bell Cave, Alabama (Parmalee 1992); +, species reported also from Ladds Quarry Cave, Georgia (Wetmore 1967; Olson 1984); #, taxa that cannot be distinguished from one or more previously listed species, and therefore not counted as a separate taxon.

Taxon	NISP	MNI	Habitat Preference
*Podilymbus podiceps – Pied-billed Grebe	3	1	A
Coragyps atratus – Black Vulture	4	2	I
*Anas cf. platyrhynchos – probable Mallard	1	1	A
Anas discors – Blue-winged Teal	1	1	A
*Anas crecca – Green-winged Teal	2	1	A
Anas strepera – Gadwall	1	1	A
Anas acuta – Pintail	2	2	A
#Anas sp. – indeterminate dabbling duck	1	0	A
Aix sponsa – Wood Duck	2	2	A
*Aythya collaris – Ring-necked Duck	2	2	A
Bucephala albeola – Bufflehead	2	1	A
Lophodytes cucullatus – Hooded Merganser	1	1	A
#cf. Mergini sp. – indeterminate diving duck	1	0	A
*#Anatidae sp. – indeterminate duck(s)	2	0	A
*Accipitridae sp. – indeterminate hawk	1	1	I
*Falco sparverius – American Kestrel	4	1	M
*Colinus virginianus – Bobwhite	3	2	M
*+Meleagris gallopavo – Wild Turkey	6	1	F
*Bonasa umbellus – Ruffed Grouse	191	26	F
*Tympanuchus cupido - Greater Prairie Chicken	30	4	G
#Tetraonidae – indeterminate grouse	31	0	I
Rallidae sp. – indeterminate rail	1	1	A
*Bartramia longicauda – Upland sandpiper	1	1	G
*cf. Catoptrophorus semipalmatus – probable Willet	1	1	I
*Scolopax minor – American Woodcock	8	1	M
#Scolopacidae sp. – indeterminate large shorebird	3	1	I
*+Ectopistes migratorius – Passenger Pigeon	35	5	F
*Otus asio – Eastern Screech Owl	16	4	F
Asio sp. – indeterminate "eared" owl	2	1	Ī
(+?) Strigidae sp. – indeterminate owl	2	2	Ī
Colaptes auratus – Northern Flicker	13	3	M
Dryocopus pileatus – Pileated Woodpecker	1	1	F
*Picoides villosus – Hairy Woodpecker	2	1	F
Melanerpes sp. – indeterminate melanerpine woodpecker	3	2	I
#Picidae sp. – indeterminate woodpecker	2	0	Ī
*Sayornis phoebe – Eastern Phoebe	8	2	M
*Cyanocitta cristata – Blue Jay	21	4	F

Table 1. (cont.)

Taxon	NISP	MNI	Habitat Preference	
Common Co	2	1	M	
Corvus brachyrhynchos – Common Crow	3	1	M	
*Corvus corax – Common Raven	3	1	F	
*Pica pica – Black-billed Magpie	1	1	M	
Pipilio erythrophthalamus - Rufous-sided Towhee	2	1	M	
Spizella passerina or Ammodramus sandwichensis –				
Chipping Sparrow or Savanna Sparrow	1	1	I	
Emberizinae sp. – indeterminate sparrow	1	1	I	
*#Passeriformes sp. – indeterminate passerines	54	4	I	
Total NISP, MNI	475	90		
Totals by habitat category				
A	23	15		
F	275	43		
G	31	5		
M	42	12		
I	104	15		

North America, the only other record in the East is from Ichetucknee River, Florida.

Modern Range in North America.—Widespread. Modern Status in Northern Georgia.—Uncommon migrant and winter visitor.

Remarks.—Based on size, these specimens probably are males, which are consistently larger than in those of any sex of the osteologically similar *Anas strepera*.

AIX SPONSA (Linnaeus) – Wood Duck Material.—2 tarsometatarsi.

Late Pleistocene Status.—This is only the fifth record; the other record in the East is from Ichetucknee River, Florida.

Modern Range in North America.—Widespread. Modern Status in Northern Georgia.—Uncommon resident and winter visitor.

Remarks.—These specimens agree with those of an adult female and a juvenile male of *Aix sponsa*, thus indicating residency of this species near the fossil site.

AYTHYA COLLARIS (Donovan) – Ring-necked Duck Material.—2 tarsometatarsi.

Late Pleistocene Status.—Widespread, although this is only the fourth record overall; the other record in

the East is from Ichetucknee River, Florida.

Modern Range in North America.—Widespread. Modern Status in Northern Georgia.—Common migrant and winter visitor.

BUCEPHALA ALBEOLA (Linnaeus) – Bufflehead Material.—Coracoid, humerus.

Late Pleistocene Status.—Widespread.

Modern Range in North America.—Widespread.

Modern Status in Northern Georgia.—Uncommon migrant and winter visitor.

LOPHODYTES CUCULLATUS (Linnaeus) – Hooded Merganser

Material.—Humerus.

Late Pleistocene Status.—Many records, mostly from Florida.

Modern Range in North America.—Widespread.

Modern Status in Northern Georgia.—Common
migrant and winter visitor.

Remarks.—Also from KSC is an eroded, fragmentary tibiotarsus referred to cf. Mergini sp. (indeterminate diving duck). Two other bones, a fragmentary humerus and tibiotarsus, cannot be identified beyond

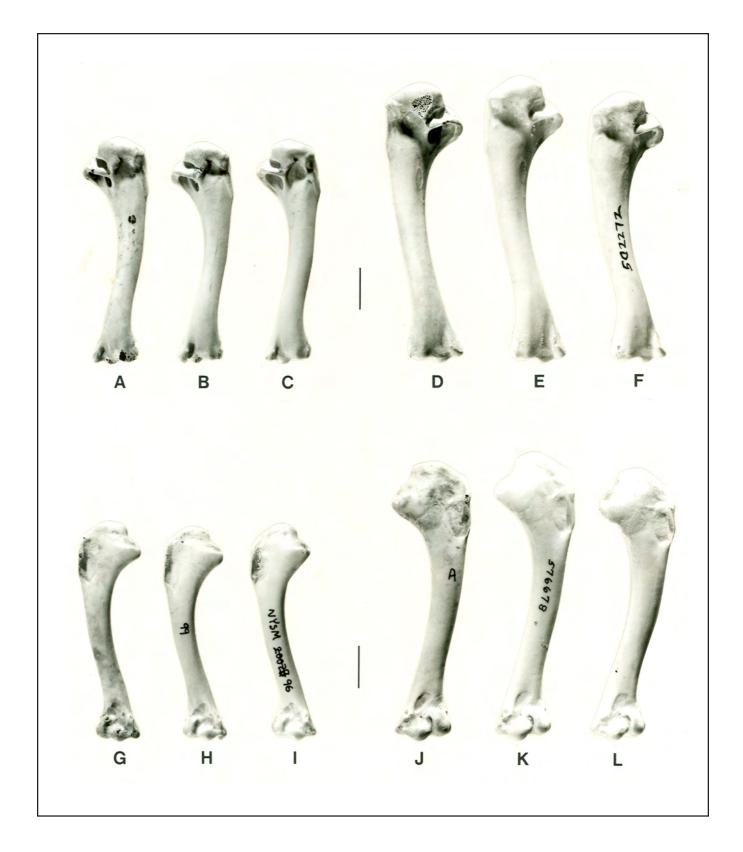


Figure 2. The humerus of grouse in ventral (A-F) and dorsal (G-L) aspects. A, G. *Bonasa umbellus*, fossil from Kingston Saltpeter Cave, Georgia. B, H. *Bonasa umbellus*, female, Maine, NYSM 99. C, I. *Dendragapus canadensis*, sex and locality unknown, NYSM 96. D, J. *Tympanuchus cupido*, fossil from Kingston Saltpeter Cave, Georgia. E, K. *Tympanuchus cupido*, male, Texas, USNM 576678. F, L. *Tympanuchus phasianellus*, male, Nebraska, USNM 502272. Scale bar = 10 mm.

Anatidae sp. (indeterminate duck).

Order ACCIPITRIFORMES (FALCONIFORMES) Family ACCIPITRIDAE

ACCIPITRIDAE sp. – indeterminate hawk

Material.—Ungual phalanx (phalanx 2 of digit I).

Remarks.—This eroded specimen is approximately the size of that in *Buteo lineatus*, *B. platypterus*, or *Circus cyaneus*, but otherwise lacks distinctive features.

Family FALCONIDAE

FALCO SPARVERIUS Linnaeus - American Kestrel

Material.—Tibiotarsus, 3 tarsometatarsi.

Late Pleistocene Status.—Widespread.

Modern Range in North America.—Widespread.

Modern Status in Northern Georgia.—Common migrant and winter visitor.

Order GALLIFORMES Family PHASIANIDAE

COLINUS VIRGINIANUS (Linnaeus) - Bobwhite

Material.—Mandible, humerus, tarsometatarsus.

Late Pleistocene Status.—Widespread.

Modern Range in North America.—Widespread. Modern Status in Northern Georgia.—Rare resident.

MELEAGRIS GALLOPAVO Linnaeus – Wild Turkey Material.—Quadrate, mandible, 2 manus phalanges, pygostyle, tarsometatarsus.

Late Pleistocene Status.—Widespread.

Modern Range in North America.—Widespread. Modern Status in Northern Georgia.—Uncommon

to common resident.

Remarks.—*Meleagris gallopavo* is the most commonly reported late Pleistocene bird in North America (Steadman 1980).

BONASA UMBELLUS (Linnaeus) - Ruffed Grouse

Material.—2 rostra, 11 mandibles, 6 quadrates, 4 furculae, 3 coracoids, scapula, 4 humeri (Fig. 2), 14 ulnae, 5 radii, 2 ulnare, 37 carpometacarpi, 8 phalanges digitalis majoris I, phalanx digitalis majoris II, 2 notaria, 3 synsacra, pygostyle, 14 femora, 16 tibiotarsi, 57 tarsometatarsi (Fig. 3).

Late Pleistocene Status.—Widespread.

Modern Range in North America.—Widespread. Modern Status in Northern Georgia.—Rare to uncommon resident.

Remarks.—Bonasa umbellus is by far the most

common bird at KSC. The same was true at Bell Cave, Alabama (Parmalee 1992). All four grouse bones from Ladds Quarry Cave were assigned to Dendragapus (Canachites) canadensis, the Spruce Grouse (Wetmore 1967). This material should be re-examined. In modern skeletons, I have been unable to distinguish consistently between D. canadensis and B. umbellus in any skeletal element other than the tarsometatarsus. Because all 57 small, well preserved tarsometatarsi were referable to B. umbellus, I provisionally refer the other skeletal elements of small grouse to that species. Also among the KSC material are a cranium, 4 rostra, 2 mandibles, 8 humeri, 2 tarsometatarsi, and 14 pedal phalanges referred to Tetraoninae sp. (indeterminate grouse). Most of this undiagnostic material probably represents B. umbellus.

The Ruffed Grouse inhabits many sorts of deciduous and mixed forests today, with little regard for level of maturity.

TYMPANUCHUS CUPIDO (Linnaeus) – Greater Prairie Chicken

Material.—Rostrum, 3 coracoids, 2 humeri (Fig. 2), 4 radii, 4 carpometacarpi, notarium, 2 pelves, 3 femora, 4 tibiotarsi, 6 tarsometatarsi (Fig. 3).

Late Pleistocene Status.—In the East, reported from three sites in Tennessee (Corgan 1974; Parmalee 1982; Parmalee & Klippel 1982) and Bell Cave, Alabama (Parmalee 1992).

Modern Range in North America.—*Tympanuchus cupido pinnatus* and *T. c. attwateri* reside locally today on the prairies of central North America. A recently extinct form, the "Heath Hen" *T. c. cupido*, lived in coastal eastern North America from at least Massachusetts to Virginia, and possibly from Maine to the Carolinas (Greenway 1967:190).

Modern Status in Northern Georgia.—No records. Remarks.—This identification is based mainly on size of the humerus, carpometacarpus, and tarsometatarsus, especially the total lengths, which seem to be diagnostic (Table 2). The bones of *T. cupido* differ from those of the closely related *T. pallidicinctus* only by averaging slightly larger. The fossils from KSC are referred to *T. cupido* rather than *T. pallidicinctus* on this basis, although some of the specimens are within the range of overlap. Among New World species of grouse, only males of *Centrocercus urophasianus* are larger than males of *T. cupido*. The tarsometatarsus in females of *C. urophasianus* is superficially similar to that in *T. cupido*, but has a more constricted central

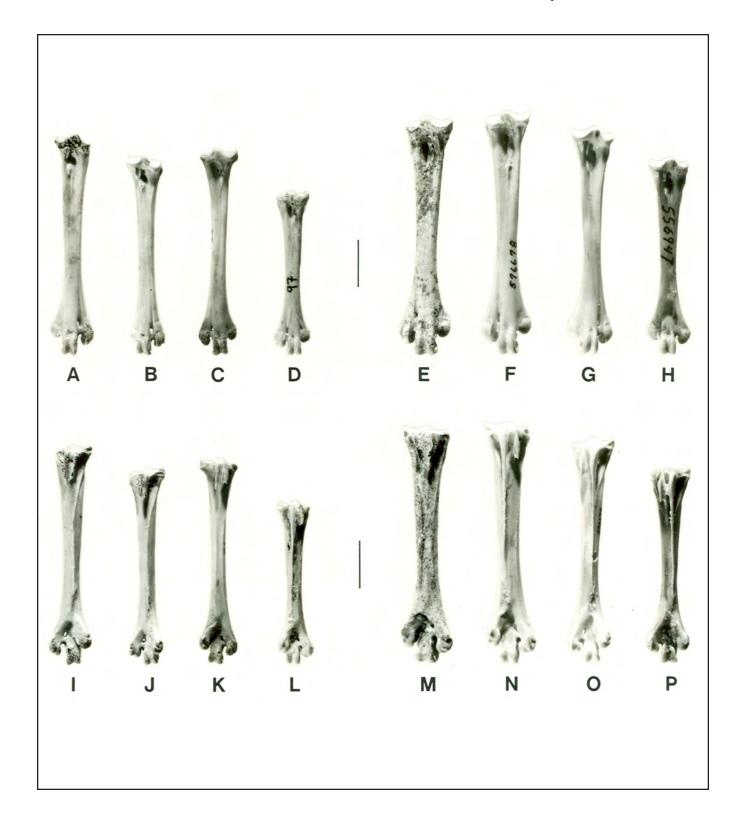


Figure 3. The tarsometatarsus of grouse in dorsal (A-H) and plantar (I-P) aspects. A, I. *Bonasa umbellus*, fossil from Kingston Saltpeter Cave, Georgia. B, J. *Bonasa umbellus*, fossil from Kingston Saltpeter Cave, Georgia. C, K. *Bonasa umbellus*, female, Maine, NYSM 99. D, L. *Dendragapus canadensis*, sex and locality unknown, NYSM 97. E, M. *Tympanuchus cupido*, fossil from Kingston Saltpeter Cave, Georgia. F, N. *Tympanuchus cupido*, male, Texas, USNM 576678. G, O. *Tympanuchus phasianellus*, male, Nebraska, USNM 502272. H, P. *Tympanuchus phasianellus*, female, Manitoba, USNM 556947. Scale bar = 10 mm.

portion of the shaft, as well as more expanded proximal and distal ends.

Order GRUIFORMES Family RALLIDAE

RALLIDAE sp. – indeterminate rail

Material.—Tibiotarsus.

Remarks.—This fragment is approximately the size of the tibiotarsus in *Rallus limicola* or *Porzana carolina*, but is otherwise undiagnostic.

Order CHARADRIIFORMES Family SCOLOPACIDAE BARTRAMIA LONGICAUDA (Bechstein) – Upland Sandpiper

Material.—Humerus.

Late Pleistocene Status.—The other eastern records are from Bell Cave, Alabama (Parmalee 1992) and Natural Chimneys, Virginia (Wetmore 1962b).

Modern Range in North America.—Widespread. Modern Status in Northern Georgia.—Rare to uncommon migrant.

Remarks.—Regardless of season, the highly migratory *Bartramia longicauda* inhabits prairies, pastures, and open fields.

cf. *CATOPTROPHORUS SEMIPALMATUS* (Gmelin) – probable Willet

Material.—Carpometacarpus.

Late Pleistocene Status.—The other eastern records are from Bell Cave, Alabama (Parmalee 1992) and Natural Chimneys, Virginia (Wetmore 1962b).

Modern Range in North America.—Locally common breeder in coastal and prairie regions; widespread migrant.

Modern Status in Northern Georgia.—Rare migrant.

Remarks.—Although this specimen agrees with *Catoptrophorus semipalmatus* in all features, it is too fragmentary for a more reliable identification.

SCOLOPAX MINOR Gmelin – American Woodcock Material.—Sternum, coracoid, 2 humeri, ulna, 2 carpometacarpi.

Late Pleistocene Status.—Four of the seven other records are from Appalachia (Parmalee 1982; Parmalee & Klippel 1982).

Modern Range in North America.—Common in the East; rare elsewhere.

Modern Status in Northern Georgia.—Uncommon

to common resident, migrant, and winter visitor.

SCOLOPACIDAE sp. – indeterminate large shorebird(s)

Material.—Furcula, 2 humeri.

Remarks.—These fragmentary specimens are approximately the size of those in *Limosa haemastica*, *Catoptrophorus semipalmatus*, or *Tringa melanoleuca*, but are otherwise undiagnostic.

Order COLUMBIFORMES Family COLUMBIDAE

ECTOPISTES MIGRATORIUS (Linnaeus) – Passenger Pigeon

Material.—Sternum, 2 coracoids, scapula, 3 humeri, 4 ulnae, 12 carpometacarpi, 4 femora, tibiotarsus, 7 tarsometatarsi.

Late Pleistocene Status.—Widespread.

Modern Range in North America.—Extinct; widespread until the late 19th century, mainly in the East.

Modern Status in Northern Georgia.—Extinct; formerly a common to abundant migrant and winter visitor.

Remarks.—*Ectopistes migratorius* occurred in great abundance in deciduous forest and mixed deciduous/coniferous forest in eastern North America throughout the Holocene until shortly before it became extinct in the early 1900s (Schorger 1955; Steadman 1988, 1998).

Order STRIGIFORMES Family STRIGIDAE

OTUS ASIO (Linnaeus) - Eastern Screech-Owl

Material.—Rostrum, 2 mandibles, 3 carpometacarpi, 2 femora, 4 tibiotarsi, 3 tarsometatarsi, ungual phalanx.

Late Pleistocene Status.—Widespread.

Modern Range in North America.—Widespread.

Modern Status in Northern Georgia.—Common resident.

ASIO sp. – indeterminate "eared" owl

Material.—Carpometacarpus, tibiotarsus.

Remarks.—These specimens represent either the Long-eared Owl, *Asio otus* or the Short-eared Owl, *A. flammeus*. The former species roosts sometimes in caves, and thus, by preying on small vertebrates, possibly contributed to the bones that accumulated in KSC.

STRIGIDAE sp. – indeterminate owl

Material.—2 tarsometatarsi (Fig. 4).

Remarks.—These specimens do not match the tar-

Table 2. The humerus, carpometacarpus, and tarsometatarsus of grouse (Tetraoninae), with mean, range, and sample size. Standard deviation is given for samples larger than 10 specimens. Measurements are in mm. F, female; M, male; U, sex unknown; LU, locality unknown.

Species, locality	Humerus		Carpo	Carpometacarpus		Tarsometatarsus	
	Total length	Proximal width	Total length	Proximal width	Total length	Proximal width	
Tympanuchus cupido fossils (U)	69.5	20.0	41.8	11.2+	47.9+	9.9	
Kingston Saltpeter Cave, Georgia	1	19.6-20.3 2	1	10.3+-12.1	45.9-52.1 6	8.6-11.3 5	
Tympanuchus cupido (M, F)	70.0	19.7	39.4	11.3	51.5	10.9	
Texas, North Dakota	65.6-72.3 8	18.5-20.7 8	37.0-41.7 8	10.5-12.0 8	49.4-53.2 8	9.8-11.8 8	
Tympanuchus pallidicinctus (M, F)	64.0	17.8	36.7	10.5	45.2	9.5	
Kansas, LU	61.3-67.7 4	17.2-18.7 4	35.0-39.7 4	10.1-10.9 2	42.6-48.4 4	9.1-10.1 4	
Tympanuchus phasianellus (M, F, U)	64.9 ± 1.9	18.6 ± 0.7	36.7 ± 1.3	10.4 ± 0.4	44.6 ± 2.0	9.8 ± 0.4	
Montana, Manitoba, South Dakota, Minnesota, Nebraska	62.4-68.2 13	17.0-20.0 13	34.6-38.8 13	9.7-11.1 13	42.1-48.7 13	9.2-10.7 13	
Centrocercus urophasianus (M)	106.9	29.7	58.3	15.5	59.0	14.5	
Montana, California	104.3-109.5 5	28.8-30.4 5	57.5-59.0 5	15.1-15.9 5	57.5-60.1 5	14.1-14.8 5	
Centrocercus urophasianus (F)	85.5	23.0	47.4	12.0	47.8	11.6	
Montana, Wyoming	84.0-86.7 4	22.6-23.8 4	46.4-48.4 4	11.6-12.2 4	46.5-49.1 3	11.4-11.9 3	
Dendragapus obscurus (F)	63.7	19.9	36.6	10.9	42.3	10.2	
Washington, Wyoming	63.4-64.0 3	19.0-20.3 3	35.7-37.9 3	10.6-11.2 3	41.5-42.8 3	10.0-10.5 3	
Dendragapus canadensis (M, F, U)	57.2	15.6	31.9	9.1	38.4	8.4	
Alaska, Alberta, LU	53.4-62.3 3	14.8-17.1 4	29.8-35.3 4	8.6-10.2 4	36.2-42.8 3	7.9-9.4 3	

Table 2. (Cont.)

Species, locality	Humerus		Carpometacarpus		Tarsometatarsus	
	Total length	Proximal width	Total length	Proximal width	Total length	Proximal width
Bonasa umbellus fossils (U)	54.3	15.5	29.9	9.1	43.8	8.1
Kingston Saltpeter Cave,	1	14.8-16.0	27.5-31.3	8.7-9.7	41.5-47.0	7.5-9.0
Georgia		3	13	13	17	21
Bonasa umbellus (M, F, U)	53.8 ± 1.5	15.8 ± 0.5	31.0 ± 0.8	9.5 ± 0.3	44.1 ± 1.4	8.2 ± 0.3
Vermont, Connecticut,	50.2-56.4	15.0-16.4	29.5-32.1	8.9-9.9	40.8-47.2	7.8-9.0
Pennsylvania, New Jersey, Virginia, Washington, D.C., West Virginia, Montana, Alaska, LU	15	15	15	14	15	15
Lagopus lagopus (M)	62.8	16.9	34.2	9.9	41.0	9.0
Alaska, Scotland	60.7-65.1	16.6-17.2	31.2-36.5	9.6-10.2	38.9-43.0	8.8-9.4
	5	6	6	6	6	6
Lagopus lagopus (F, U)	59.1	15.7	33.0	9.3	38.3	8.4
Alaska, Scotland	55.9-61.4	15.4-15.9	31.5-36.5	8.8-9.8	37.4-39.1	8.1-8.7
	3	4	4	4	3	4
Lagopus mutus (M, F, U)	57.6 ± 2.8	15.7 ± 1.0	32.3 ± 1.4	9.4 ± 0.5	32.5	7.6
Alaska, Northwest Territory,	53.1-62.7	14.3-17.2	29.7-34.4	8.6-10.1	30.4-34.8	7.1-8.2
British Columbia	10	10	10	10	10	10

sometatarsus of any living species of New World Owl and may represent the extinct, undescribed species of owl that Olson (1984) reported from a single mandibular symphysis from nearby Ladds Quarry Cave. Olson regarded this specimen as an inadequate basis for describing a new species and the two tarsometatarsi from KSC, being from very young juveniles, are likewise insufficient.

The mandibular symphysis from Ladds was larger than in any living species of owl, but was closer qualitatively to Strix than to Bubo or Nyctea (Olson 1984). The specimens from KSC (Fig. 4) are so immature that generic characters are nearly impossible to discern. They are much larger than the tarsometatarsus of any species of Surnia, Otus, Glaucidium, Aegolius, Micrathene, or Athene. They are stouter than in Strix varia, S. nebulosa, S. occidentalis, Bubo virginianus, or any species of Tyto, Asio, Ciccaba, Pulsatrix, or Rhinoptynx. In stoutness, they agree more closely with the tarsometatarsus in Nyctea scandiaca, although they are much shorter (Fig. 4). Unfortunately, no available specimen of N. scandiaca was of a similar stage of immaturity. The great relative stoutness of the KSC specimens is seen in their total lengths and minimum widths (in mm) of 28.9, 7.0, and 26.0, 5.8. The smaller specimen is from a slightly less mature individual. The same measurements in the juvenile specimens illustrated in Figure 4 are 49.3, 6.0 mm (*Strix varia*), 54.7, 8.9 mm (Nyctea scandiaca), and 59.7, 7.1 mm (Bubo bubo).

In summary, the two juvenile strigid tarsometatarsi from KSC are somewhat similar to those in *Nyctea scandiaca* among living owls, but are much shorter and proportionally even stouter. If they represent the extinct, undescribed owl that Olson (1984) reported from nearby Ladds Quarry Cave, then the tarsometatarsus was small relative to the mandible, even if the tarsometatarsi represent males and the mandible was from a female. Regardless of the species represented, the two juvenile specimens from KSC indicate local nesting for this enigmatic owl, which therefore may have contributed to the faunal accumulation at KSC.

Order PICIFORMES Family PICIDAE

COLAPTES AURATUS (Linnaeus) - Flicker Material.—Mandible, 2 coracoids, 2 humeri, 5 ulnae, 3 carpometacarpi.

Late Pleistocene Status.—Widespread.

Modern Range in North America.—Widespread.

Modern Status in Northern Georgia.—Common

resident and winter visitor.

Remarks.—Two of the ulnae are from juveniles, thereby indicating local residency at the time of fossil deposition.

DRYOCOPUS PILEATUS (Linnaeus) – Pileated Woodpecker

Material.—Tibiotarsus.

Late Pleistocene Status.—Five of the seven previous records are from Appalachia.

Modern Range in North America.—Widespread.
Modern Status in Northern Georgia.—Common but local resident.

Remarks.—This specimen agrees qualitatively with the tibiotarsus of *Dryocopus pileatus* rather than that of any other North American woodpecker, including the Neotropical *D. lineatus*. The specimen is at the low end of the size range for *D. pileatus*, having a total length of 46.7 mm, compared with a range of 46.7-53.7 mm for modern specimens from various localities (N = 21, both sexes, with males averaging larger than females). The single modern specimen that was the same size as the KSC fossil was USNM 19346, an unsexed but probable female from West Virginia.

PICOIDES VILLOSUS (Linnaeus) – Hairy Woodpecker Material.—Sternum, humerus.

Late Pleistocene Status.—The only other records are from Bell Cave, Alabama (Parmalee 1992) and Clarks Cave, Virginia (Guilday et al. 1977).

Modern Range in North America.—Widespread. Modern Status in Northern Georgia.—Uncommon resident.

MELANERPES sp. – indeterminate melanerpine woodpecker

Material.—2 ulnae, tibiotarsus.

Remarks.—These specimens cannot be distinguished from the same elements in *Melanerpes carolinus*, the Red-bellied Woodpecker, or *M. erythrocephalus*, the Red-headed Woodpecker, both of which occur today in northern Georgia. Also from KSC are a fragmentary humerus and tibiotarsus referred to Picidae sp. (indeterminate small woodpecker).

Order PASSERIFORMES Family TYRANNIDAE

SAYORNIS PHOEBE (Latham) – Eastern Phoebe Material.—Sternum, coracoid, 3 humeri, ulna, carpometacarpus, tarsometatarsus.

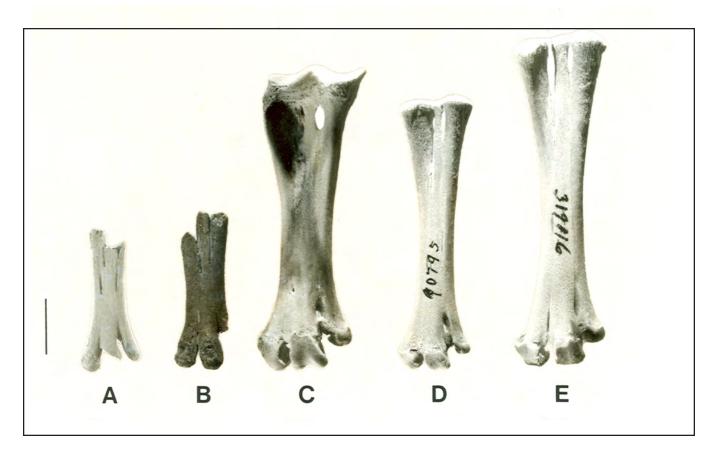


Figure 4. The tarsometatarsus of owls in dorsal aspect. A, B. Fossils of Strigidae sp. from Kingston Saltpeter Cave, Georgia. C. *Nyctea scandiaca*, female, Alaska, USNM 502135. D. *Strix varia*, sex unknown, Illinois, USNM 90795. E. *Bubo bubo*, sex unknown, China, USNM 319116. Scale bar = 10 mm.

Late Pleistocene Status.—The only other records are from Bell Cave, Alabama (Parmalee 1992), Cheek Bend Cave, Tennessee (Parmalee 1982; Parmalee & Klippel 1982), Natural Chimneys, Virginia (Wetmore 1962b), and Brynjulfson Cave II, Missouri (Parmalee & Oesch 1972).

Modern Range in North America.—Widespread. Modern Status in Northern Georgia.—Common resident, migrant, and winter visitor.

Remarks.—Tyrannids are rarely reported as fossils. With 10 species of tyrannids found regularly in Georgia today, I will present osteological evidence to distinguish *Sayornis phoebe* from other flycatchers of eastern North America. In each of the elements reported, *S. phoebe* is smaller than in any species of *Tyrannus* or *Myiarchus* and larger than in *Contopus virens* or any species of *Empidonax*. The same elements in *Contopus* ("*Nuttallornis*") borealis are roughly similar in size to those of *S. phoebe*, but the latter is distinguished as follows: sternum – deeper and more

curved keel, shorter bifurcations on spina externa; coracoid – greater pneumaticity on both the sternal and humeral end; humerus, ulna, and carpometacarpus – shaft more slender; tarsometatarsus – longer, more slender. Because it often nests at the mouths of caves, *Sayornis phoebe* is more common than most other passerines in late Quaternary cave deposits (Steadman et al. 1993).

Family CORVIDAE

CYANOCITTA CRISTATA (Linnaeus) – Blue Jay Material.—Mandible, 6 humeri, 3 ulnae, 3

Material.—Mandible, 6 humeri, 3 ulnae, 3 carpometacarpi, 3 tibiotarsi, 5 tarsometatarsi.

Late Pleistocene Status.—Of seven other records, four are from Appalachia, two from Florida, and one from Missouri (Brodkorb 1978; Emslie 1998).

Modern Range in North America.—Widespread. Modern Status in Northern Georgia.—Common resident, migrant, and winter visitor.

Remarks.—All of these specimens match those of modern skeletons of *Cyanocitta cristata*, although

while making these comparisons I was struck by the osteological similarity between *Cyanocitta cristata* and *Cyanocorax yncas*, the Green Jay, a Neotropical species whose modern northern range limit is southern Texas. As other species of birds and mammals of tropical Gulf Coast affinities have been reported from late Pleistocene sites in eastern North America (Lundelius et al. 1983; Emslie 1998), it seemed appropriate to investigate the possible occurrence of *Cyanocorax yncas* in greater detail.

The mandibles of Cyanocorax yncas and Cyanocitta cristata are readily told from those of all other North American jays by their overall broadness, especially in the mandibular symphysis. The mandible from KSC is referred to Cyanocitta cristata because of the similar placement of the scars for attachment of the adductor muscles on the dorsal surface of the ramus. However, the mandibles of the two species in question can be extremely similar, perhaps indistinguishable, in certain individuals. The mandible of Cyanocorax yncas averages smaller than that of Cyanocitta cristata, although there is much overlap, in which range the KSC fossil lies. The postcranial elements of the two species cannot be distinguished consistently. I see no osteological basis for maintaining these two species in different genera. Although I am rather confident that the fossils from KSC are correctly referred to Cyanocitta cristata, I would add that this is done as much on geography (a dangerous practice in paleontology) as osteology. A thorough comparative osteology of New World jays is needed to provide a solid basis for fossil identification.

CORVUS BRACHYRHYNCHOS Brehm – Common Crow

Material.—Ulna, carpometacarpus, femur.
Late Pleistocene Status.—Widespread.
Modern Range in North America.—Widespread.
Modern Status in Northern Georgia.—Common resident.

Remarks.—These elements are larger than those of *Corvus ossifragus*, the Fish Crow, and smaller than those of *C. corax*, the Common Raven.

CORVUS CORAX Linnaeus – Common Raven Material.—Carpometacarpus, 2 ungual phalanges. Late Pleistocene Status.—Although commonly reported from the West, the only other record in the East is from Bell Cave, Alabama (Parmalee 1992).

Modern Range in North America.—Widespread in the West, and in the East north of 45°N; local but increasing in Appalachia.

Modern Status in Northern Georgia.—Rare, local resident.

Remarks.—These fossils differ from those of congeners by their larger size. The carpometacarpus is from a juvenile, indicating that Corvus corax nested near KSC at the time of fossil deposition. In eastern North America, C. corax is confined historically to the Appalachian Mountains, from northern Georgia through Maine, and to the boreal forests of Canada and northernmost United States. Destruction of the eastern deciduous forest during the 19th and 20th centuries badly fragmented the range of C. corax. Late Holocene fossils of C. corax have been reported from the Hiscock Site, western New York, in a flat region 30 km south of Lake Ontario (Steadman 1988). This shows that C. corax was not confined prehistorically just to the mountainous areas in the East. In much of Appalachia today, C. corax is reclaiming much of its former range as forests mature (Boarman & Heinrich 1999).

PICA PICA (Linnaeus) – Black-billed Magpie Material.—Quadrate (Figure 5).

Late Pleistocene Status.—Four of the five other records from the East are from southern Appalachia, namely Natural Chimneys, Virginia (Wetmore 1962a, b, c), Strait Canyon, Virginia (Eshelman & Grady 1986; P. W. Parmalee, pers. comm.), Baker Bluff Cave, Tennessee (Guilday et al. 1978), and Bell Cave, Alabama (Parmalee 1992). The fifth is from Cutler Hammock, Florida (Emslie 1998).

Modern Range in North America.—West and North-central.

Modern Status in Northern Georgia.—No records. Remarks.—Among North American corvids, this complete left quadrate is larger than that in Cyanocitta cristata, C. stelleri, Cyanocorax yncas, Perisoreus canadensis, or any other "jay" (Aphelocoma, Gymnorhinus) and is smaller than that in Corvus brachyrhynchos, C. cryptoleucus, or C. corax. It is roughly the size of that in Corvus ossifragus, but agrees with that in Pica pica rather than C. ossifragus in these characters: junction of orbital process and jugal process forms a more obtuse angle and is more curved; proximal portion of orbital process has a sharp ridge on ventral surface (rounded in C. ossifragus); lateral surface of shaft of otic process is more sharply edged; angle formed at junction of jugal process and otic process is less obtuse, i.e., more perpendicular; body of quadrate is slightly but distinctly excavated just dorsad of mandibular articulation; and, in medial aspect, the shaft of orbital process is more tapered, i.e., wider proximally and narrower distally (width more uniform in *C. ossifragus*).

The quadrate from KSC also resembles in size that of Nucifraga columbiana, Clark's Nutcracker of western North America, but agrees with that in Pica pica as follows: lateral surface of shaft of otic process more sharply edged; angle formed at junction of jugal process and otic process more abrupt (more rounded in N. columbiana); and, in ventral aspect, mandibular articulation less protrudent ventrally and more oblong, i.e., less rounded. Lastly, the KSC fossil is roughly similar in size to that in four large species of Neotropical jays (Calocitta formosa, Psilorhinus morio, Cissilopha sanblasiana, and Cissilopha yucatanicus), but agrees with that in Pica pica as follows: large ventral knob on shaft of jugal process absent; angle formed at junction of jugal process and otic process more obtuse; and otic process more slender.

Aside from the characters just outlined, the fossil agrees with modern specimens of $Pica\ pica$ in size, with a length through the otic process and mandibular articulation of 9.7 mm (in 47 modern specimens of both sexes, range = 8.3-10.1 mm, mean = 9.2 mm) and a width across the body (from junction of orbital process and mandibular articulation to junction of jugal process and otic process) of 5.4 mm (in 47 modern specimens of both sexes, range = 4.5-5.6 mm, mean = 5.0 mm).

Pica pica occurs today in western North America and much of Eurasia. It is a bird of open areas with a cool temperate climate. Natural grasslands, cultivated fields, and open brushlands are the favored foraging habitat of *P. pica*, which nevertheless requires trees or hedgerows for nesting. It is often common where open habitats are interrupted by wooded riparian corridors, shelterbelts, and patchy forests or woodlands. In North America, *P. pica* does not nest regularly east of 95° W longitude, although stray birds are encountered rarely in the eastern United States, mainly in the fall or winter. Eastern Colorado and northeastern New Mexico are the localities nearest to Georgia where the species nests today.

Family EMBERIZIDAE PIPILO ERYTHROPHTHALMUS (Linnaeus) –

Rufous-sided Towhee

Material.—Rostrum, mandible.

Late Pleistocene Status.—The nearest to KSC of five other records is from Cheek Bend Cave, Tennessee (Parmalee 1982; Parmalee & Klippel 1982).

Modern Range in North America.—Widespread.

Modern Status in Northern Georgia.—Common resident, migrant, and winter visitor.

SPIZELLA PASSERINA (Bechstein) – Chipping Sparrow or AMMODRAMUS SANDWICHENSIS

(Gmelin) – Savanna Sparrow

Material.—Mandible.

Remarks.—This mandibular symphysis lacks both rami. Species-level identification of this small sparrow would be possible with a more complete specimen.

EMBERIZINAE sp. – indeterminate sparrow Material.—Rostrum.

Remarks.—This specimen, lacking the distal onethird, is approximately the size of the rostrum in a medium-sized sparrow such as *Melospiza melodia*, the Song Sparrow, but is too fragmentary for species-level identification.

PASSERIFORMES sp. – indeterminate passerines

Material.—3 sterna, 5 coracoids, 14 humeri, 5 ulnae, 7 carpometacarpi, 2 femora, 10 tibiotarsi, 7 tarsometatarsi.

Remarks.—These postcranial specimens, none of which is larger than in *Cyanocitta cristata*, mainly represent small and medium-sized oscines. Because of the great variety of passerines in Georgia and their osteological similarities, I have not tried to identify these specimens further.

DISCUSSION AND CONCLUSIONS

Many different predators, both avian and mammalian, may have contributed to accumulating the avian fossils at Kingston Saltpeter Cave. Which species were involved is difficult to determine because predatory or scavenging birds such as vultures, condors, ravens, owls, and falcons can deposit bones in caves while leaving behind few if any of their own remains. Regardless, the species-level composition of the KSC avifauna is biased as a result of the feeding preferences of predators and scavengers that accumulated the bones.

Like so many late Pleistocene vertebrate faunas of the Appalachian region, the KSC bone deposit is not well stratified. Thus I cannot be certain that, about 15,000 to 12,000 years ago, the relatively northern or western species of birds discovered at KSC, such as the Ruffed Grouse, Prairie Chicken, Common Raven, and Black-billed Magpie, were contemporaneous with what we regard today as more southern species of am-



Figure 5. The quadrate of *Pica pica* in medial aspect. A. Fossil from Kingston Saltpeter Cave, Georgia. B. Modern specimen, sex unknown, Wyoming, USNM 19420. Scale bar = 10 mm.

phibians and reptiles such as a frog *Gastrophryne* carolinensis, lizard *Anolis carolinensis*, and snake *Virginia valeriae* that Leslie Fay (pers. comm.) has identified from KSC. Nevertheless, such "disharmonious" or "non-analog" associations of species are typical of late Pleistocene floras and vertebrate faunas in the southeastern and southwestern United States (Cole 1995; Stafford et al. 1999).

Several major habitat types are suggested by the birds of KSC, which are very similar to those inferred by the birds identified at Bell Cave, Alabama (Parmalee 1992). I have assigned habitat preferences to each taxon in Table 1. The aquatic species (grebes, rails, ducks, certain shorebirds; total NISP, MNI = 23, 15) are characteristic of shallow, standing water such as that in, or at the edge of, a marsh or shallow lake. The landbirds include species that prefer forests, those found only in grasslands, and those of more wide-ranging habitat tolerances. The avifauna is dominated by species in the forest category, such as Wild Turkey, Ruffed Grouse, Passenger Pigeon, Eastern Screech-Owl, Pileated Woodpecker, Hairy Woodpecker, and Blue Jay (total NISP, MNI = 275, 43). Each of these species may live either in deciduous forests or mixed deciduous/coniferous forests. In the grassland category are Prairie Chicken and Upland Sandpiper (total NISP, MNI = 31, 5). Most of the remaining species (total NISP, MNI = 42, 12) tend to prefer mixtures of forest or brushland with open areas.

In spite of the dominance of forest species, it is

clear that northern Georgia was a region of environmental heterogeneity in the late Pleistocene. Among the 19 species shared between KSC and Bell Cave, Alabama (Parmalee 1992; Table 1 herein), seven prefer forest, five are aquatic, five are of varied habitat preference, and two prefer grasslands. Thus the environmental heterogeneity suggested by the KSC avifauna was not just a local phenomenon.

The habitat inferences of the birds from Kingston Saltpeter Cave also agree fairly well with paleobotanical evidence from the piedmont and mountains of the Southeast. The proposed dominant late Pleistocene habitats in this region were pine/spruce/fir forests or woodlands, with deciduous trees such as oaks and hickories also occurring, as well as localized prairies and sandhill communities (Watts 1970, 1983; Jackson & Whitehead 1993; Webb et al. 1993). Among the fossil birds from KSC, forest-loving species far outnumber those that prefer open areas, both in numbers of species and in numbers of individuals. This suggests that forests and woodlands dominated the upland regions of northern Georgia in late Pleistocene times. The high incidence at KSC of birds that eat mast (ruffed grouse, turkeys, passenger pigeons, blue jays) also would suggest a strong deciduous element (oaks, beech, chestnut) in the late Pleistocene forests of southernmost Appalachia.

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