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The Irvingtonian Avifauna of Cumberland Bone Cave, Maryland

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Abstract

The early and mid-Pleistocene avian communities of North America are best known from the Rocky Mountain region and peninsular Florida. In the Appalachian Mountain region, only a small number of avian bones from mid-latitude cave deposits have been attributed to this time period. Here, I enlarge this record by reporting on bird bones from Cumberland Bone Cave in western Maryland, a well-known locality for large and small Irvingtonian mammals and other vertebrates. The taxa identified encompass ground birds, waterfowl, a hawk, two eagles, a vulture, an owl, a jay, a flycatcher, a junco or sparrow, and a finch. No purely boreal elements are confirmed as part of the avian assemblage, and all of the extant species that are positively or tentatively identified in the assemblage still occur in the region today. An immature bone referred to the Black Vulture (*Coragyps atratus* (Bechstein)) represents an Irvingtonian breeding record for the species in Maryland. This record occurs at the northern limit of the current breeding range for the genus. Extinct species in the assemblage include the Passenger Pigeon (*Ectopistes migratorius* (Linnaeus)), a large screech owl (*Megascops guildayi* (Brodkorb & Mourer-Chauviré 1984)), and the large goose, *Branta dickeyi* Miller 1924. It can be argued that none of these represent the extinction of a phyletic lineage during the Irvingtonian. Based on the broad habitat preferences of modern counterparts of the birds in the assemblage, we can expect that Irvingtonian habitats near the site included mixed forest with mast-producing hardwoods and both early and later successional stages represented. There must have been fluvial, wetland, or lacustrine habitat suitable for waterbirds nearby, and probably also open woodland or grassy savannah areas, suitable for vulture foraging, turkey nesting, and booming by Ruffed Grouse.

Key words: mid-Pleistocene, fossil birds, paleoecology, extinction, *Branta dickeyi, Bonasa umbellus, Coragyps atratus, Ectopistes migratorius, Megascops guildayi*

Introduction

The bone deposits at Cumberland Bone Cave in Alleghany County, Maryland, were discovered in 1912 during dynamite blasting to create a roadbed for the Western Maryland Railway. Located in the Valley and Ridge Physiographic Province, at the base of a limestone ridge near Corriganville (39.69 deg. N, 78.79 deg. W, 245 m asl), the site soon became recognized as a major locality for Pleistocene mammals of the mid-latitude Appalachian Mountains (Gidley 1914, 1920; Gidley & Gazin 1938). The diverse assemblage of mammals from the cave correlates with the Irvingtonian North American Land Mammal Age, which covers the early to mid-Pleistocene from roughly 1.9 to 0.15 Ma (Bell *et al.* 2004; Cohen & Gibbard, 2011). Arvicoline biochronology suggests that the age of bone accumulation can be further narrowed to a division of the Irvingtonian termed Irvingtonian II, estimated to range from 0.85 to 0.4 Ma (Bell 2000; Bell *et al.*, 2004). Coupled uranium-series and electron spin resonance dating of two fossil peccary (*Platygonus* sp. Le Conte 1848) teeth offer more precise age estimates of 722±64 ka and 790±53 ka for the fossil accumulation (Withnell *et al.* in press). These dates are consistent with paleomagnetic evidence of speleothem growth in the cave prior to the Brunhes-Matuyama reversal in the earth's magnetic polarity (i.e., prior to 780 ka; Withnell *et al.* in press).

Two previous papers reported on bird bones from the site: Wetmore (1927) identified a single avian bone as a Ruffed Grouse (*Bonasa umbellus* (Linnaeus)), and Brodkorb & Mourer-Chauviré (1984) identified six bones as representing six additional species of birds, notably including the extinct Passenger Pigeon (*Ectopistes migratorius*) and a new species of owl (*Megascops guildayi*). Brodkorb & Mourer-Chauviré identified a tarsometatarsus from the site as a Canada Jay, (*Perisorius canadensis* (Linnaeus)), and interpreted the presence of this species as evidence of

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a cooler climate compared with the present. Based on the presence of *P. canadensis*, Brodkorb & Mourer-Chauviré thought it likely that the deposit accumulated during a glacial stage, most likely the Illinoian which extends from about 130 ky to perhaps as long ago as 300 ky (Cohen & Gibbard 2011). However, as noted above, other data favor an earlier age for the site.

I studied and catalogued a larger group of bird bones that were collected from Cumberland Bone Cave in the 1990s and 2000s. I also reexamined four of the seven bird bones reported from the site in previous literature. Here, I present taxonomic identifications of the avian fossils from Cumberland Bone Cave and discuss the assemblage in terms of inferred nearby habitats when the bones were accumulating and avifaunal turnover in the mid-latitude Appalachians since then.

Materials and methods

All fossil specimens are housed at the Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC (PAL USNM), except the six bones in Brodkorb & Mourer-Chauviré's report, which are at the Carnegie Museum of Natural History, Pittsburgh, PA (CM). The newly reported bones in this report were collected from the site by Trent Spielman. Frederick V. Grady sorted the collection according to higher taxonomic groups and freed some of the bones from breccia by acid etching at the Vertebrate Paleontology Preparation Laboratory of NMNH.

The fossils were identified based on comparisons with the skeleton collection of the Bird Division, Department of Vertebrate Zoology, NMNH. Avian body masses compiled by Dunning (2008) were useful for selecting species of roughly similar body size to the fossil taxa, within families or orders, for further comparisons. Bone measurements were taken with a digital caliper and rounded to the nearest 0.1 mm. Taxonomic nomenclature follows the American Ornithological Society Checklist of North and Middle American Birds (Chesser *et al.* 2019). Taxonomic authorities are given on first mention with dates and full references provided for the fossil taxa only. For extant taxa, dates and taxonomic authorities can be found in prior published editions of and supplements to the Checklist cited above. The letters l and r indicate left and right side of the body; f and m indicate female and male. In taxonomic attributions, cf. indicates the specimen is referred to the named taxon, and aff. indicates only that the specimen has affinities with the named taxon. Anatomical nomenclature follows Baumel & Witmer (1993), with many terms translated into English vernacular.

Statistics were calculated in R version 3.6.1 (2019-07-05) (R Core Team 2019), using the RStudio interface (RStudio Team 2018) and the stats package. Principal components analysis was performed using the function prcomp, with variables log-transformed and normalized (scaled to have unit variances and centered on zero). Graphics were produced using the ggplot2 package (Wickham 2016). Box-and-whisker plots show the medians, lower and upper quartiles, ranges, and outliers of the distributions. Plots of principal components were produced using the function ggbiplot v0.55.

Comparative material examined

The following skeletons in the collection of the Bird Division at NMNH (catalog acronym USNM BIRDS), were examined and/or measured: *Coscoroba coscoroba* (Molina) 345438 m, 291255 f; *Cygnus buccinator* Richardson 492496 m, 347734 f; *C. columbianus* (Ord) 488538, 499393; *C. melanocoryphus* (Molina) 428167 m (captive), 345227 m (captive); *Anser albifrons* (Scolopi) 488745 f; *A. rossi* Cassin 430474 f; *A. canagicus* (Sevastianov) 638783 m; *A. caerulescens* (Linnaeus) 501617 f; *Branta canadensis* (Linnaeus) 343185 m (captive), 343006 m (captive), 488182 m, 488488 m, 488723 m, 489759 m, 610626 m, 488584 f, 555497 f (captive), 561860 f, 599464 f (captive); *B. hutchinsii* (Richardson) 630938 m, 430286 m; *Oxyura jamaicensis* (Gmelin) 492491 m, 499639, 623361; *Anas crecca carolinensis* Gmelin 610635 f, 431027 f, 610632 m, 638839; *Spatula discors* (Linnaeus) 502641 f, 502643 m, 502645 m, 562841 m; *Bucephala albeola* (Linnaeus) 492434 m, 632035 f, 644552; *Meleagris gallopavo* Linnaeus 19634 m, 556311 m, 556360 m, 501019 f, 556334 f; *Tympanuchus cupido* (Linnaeus) 576677 f; *T. c. cupido* 319417; *Bonasa umbellus* 559643 m, 563661 m, 621367 m, 641459 m, 557528 f, 641448 f; *Falcipennis canadensis* (Linnaeus) 641435 m, 641460 m, 641432 m, 641444 m, 641446 f, 557527 f; *Lagopus leucurus*

(Richardson) 640234; *L. mutus* (Montin) 641084 m*, L. lagopus* (Linnaeus) 622651 m; *Cathartes aura* (Linnaeus) 621554, 644556; *Coragyps atratus* 500989 m, 622507 m, 647497 m, 647499 m, 623354 f, 647498 f, 647500 f; *Haliaeetus leucocephalus* (Linnaeus) 698, 2422, 8605, 19718, 611746 m, 615007 m, 611753 f, 611754 f immature, 611757 f immature; *Circus cyaneus* (Linnaeus) 291684 m, 291187 m immature, 489908 f; *Accipiter cooperi* (Bonaparte) 636924 m, 614341 m imm., 553854 f, 612006 f, 623631 f; *Accipiter gentilis* (Linnaeus) 290342 m; *Buteo lineatus* (Gmelin) 614338 m; *B. platypterus* (Viellot) 610745 m; *B. lagopus* (Pontoppidan) 499426 f; *Aquila chrysaetos* (Linnaeus) 491476 m, 19394, 18194, 612086; *Falco peregrinus* Tunstall 553620 m; *Tyto alba* (Scopoli) 553887 m; *Strix varia* Barton 556919 f; *Asio otus* (Linnaeus) 554126 m, 555706 f, 553816 f; *Asio flammeus* (Pontoppidan) 499484 m, 614841 m, 499485 f, 610423 f; *Megascops asio* (Linnaeus) 502024 m, 556918 m, 610966 f; *M. kennecottii* (Elliot) 621106 m, 637719 m, 637702 f, 641659 f; *Aegolius funereus* (Linnaeus) 623663 m; *Surnia ulula* (Linnaeus) 622484 m, 610388 m; *Athene cunicularia* (Molina) 610970 m, 630744 m; *Patagioenas fasciata* Say 499473 m, 499472 f; *P. leucocephala* (Linnaeus) 554982 m; *P. cayennensis* (Bonnaterre) 562537 sex unknown; *P. maculosa* (Temminck) 630267 f; *Ectopistes migratorius* 18520 (complete), 292904 sex unknown (complete), 224320 m (partial), 224319 m (partial), 224322 m (partial); *Zenaida asiatica* (Linnaeus) 642168 m, 646526 f; *Z. macroura* (Linnaeus) 490801 f, 491239 m, 622529 f; *Z. aurita* (Temminck) 554975 m; *Sayornis phoebe* (Latham) 489807 m; *Cyanocitta stelleri* (Gmelin) 614422 f; *Cyanocitta cristata* (Linnaeus) 499266 m, 614424 f hatch year based on skull ossification, 614427 m, hatch year based on skull ossification; *Perisoreus canadensis* 622673 f, 489846 m; *Aphelocoma coerulescens* (Bosc) 614082 m; *A. californica* (Vigors) 489825 m, 641219 f; *A. woodhouseii* (Baird) 614433 m, 346480 f; *Riparia riparia* (Linnaeus) 499691 m, 490504 f; *Tachyineta bicolor* (Viellot) 499694 m; *Toxostoma rufum* (Linnaeus) 17710; *Coccothraustes vespertinus* (Cooper) 490800 f; *Pinicola enucleator* (Linnaeus) 489737 m, 502668 m; *Molothrus ater* (Boddaert) 634899 m; *Quiscalus quiscula* (Linnaeus) 502026 m 502008 f; *Pheucticus ludovicianus* (Linnaeus) 553159 m; *Cardinalis cardinalis* (Linnaeus) 611386 m; *Passerina caerulea* (Linnaeus) 642184 m, 499098 m, 642137 m. Specimens examined are adults unless otherwise noted; sex is given if known. Additional skeletons in the Bird Division's collection were briefly consulted and/or measured to narrow down identifications and evaluate intraspecific variability.

Systematic Paleontology

Below, I present a taxonomic list with descriptions of identification criteria and remarks about the fossil bird bones from the cave, including those previously identified by Wetmore (1927) and Brodkorb & Mourer-Chauviré (1984).

Aves

Anseriformes

Anatidae

Anserinae

Branta dickeyi Miller, 1924

Material. USNM PAL 641972, r carpometacarpus: proximal end with damage to trochlea carpalis, collected July 2002 (Fig. 1F).

Description. A large anserine carpometacarpus with a long extensor process of the alular metacarpal that is perpendicular to the long axis of the bone and narrows distinctly towards the tip. In contrast, the extensor process is shorter in *Chen* and *Anser*; and shorter and wider at the tip in *Coscoroba* and *Cygnus*. The fossil agrees well in morphology with the largest comparative skeletons of *Branta canadensis* but exceeds them in size (at least if skeletons of captive-reared individuals are excluded from comparisons). It is distinctly larger than other North American species of Anserinae. The extensor process resembles large individuals of *B. canadensis* in being long and robust. Rough-surfaced exostoses are present at the tip of the extensor process; these tend to be present in large males of *B. canadensis* but can also occur in other Anseriformes.

Measurements. In the fossil, the maximum depth from the carpal trochlea through the extensor process is 28.6 mm. This exceeds the range for 12 modern carpometacarpi of *B. canadensis* measured by Emslie (1995; range 21.8-25.8) and nine measured by me (range 19.8–25.3, including two from South Dakota, within the original range of the largest subspecies of Canada Goose, *B. canadensis maxima* Delacour). It closely matches the measurements recorded by Emslie (1995) for two Irvingtonian fossil carpometacarpi of the fossil species *Branta dickeyi*, one from Florida and one from Oregon, both of which measured 28.7 mm.

Remarks. The large fossil goose *B. dickeyi* has the osteological characteristics of *Branta* but is roughly the size of a Tundra Swan (*C. columbianus*). It has previously been reported from three disparate localities in North America: the Rancholabrean McKittrick tar seeps of California (Miller 1924), a Blancan locality in Malheur County, Oregon (Miller 1944), and an early Irvingtonian locality in Florida (Leisey Shell Pit, Emslie 1995). There are few complete bones among these fossils, and not many bones from each locality. I have ascribed the large but fragmentary carpometacarpus of *Branta* from Cumberland Bone Cave to the species, although this does require the assumption that incomplete remains from widely separated localities represent a single species.

In the Oregon and Florida sites, *B. dickeyi* co-occurs with smaller *Branta* fossils that match *B. canadensis* in size. This supports the view that the fossil species represents an extinct phyletic lineage rather than a chronospecies of its modern relative. However, if we consider the modern species *B. canadensis* as a potential modern analog, interpreting the fossils becomes more complex. *B. canadensis* is migratory within North America and exhibits considerable geographic variation in body size across its broad range (Aldrich 1946; Delacour 1951). Populations that breed at high latitudes in northern Canada and Alaska tend to migrate farther than, and to be smaller in body size than, those that breed at mid-latitudes (Mowbray *et al.* 2002). (This is independent of the human-mediated expansion in the distribution of large-bodied, resident Canada Geese that began in the 1960s due to captive propagation and release (Ankey 1996; Mowbray *et al.* 2002.)) Such a pattern of size variation and migration could theoretically cause individuals of the same species, but quite different body sizes, to be present in the same fossil site.

The largest modern subspecies of Canada Goose, *B. canadensis maxima* Delacour, bred in the Great Plains well west of Cumberland Bone Cave and was thought to be extinct when it was described (Delacour 1951). A small population of these birds was discovered in 1962 and taken into captive propagation. Releases of the captive-reared birds into the wild after habituation to human-modified habitats enabled them to expand in geographic distribution, become resident year-round in many regions, and increase exponentially in population size (Ankey 1996; Mowbray *et al*. 2002). Some captive-reared individuals of this subspecies in the USNM collection approach *B. dickeyi* in skeletal size, although it is unclear whether birds with no history of captivity attain the same body size. In ascribing the Cumberland Bone Cave fossil to *B. dickeyi*, I have followed the lead of prior authors and have left unresolved the question of whether the fossils of this species represent larger-bodied populations that are ancestral to modern *B. canadensis*.

Anatinae

Anatinae, aff. *Anas crecca carolinensis/Spatula discors*

Material. CM 34027, l carpometacarpus: proximal end lacking most of the alular metacarpal.

Description. Smaller in size than all but the smallest group of anatids (Table 1). Larger than *Oxyura jamaicensis* and with a deeper fossa distal to the pisiform process and the carpal trochlea less narrow and blade-like. Larger than *Bucephala albeola*, with the shaft of the major metacarpal wider and with a different configuration of rugosities in the supratrochlear fossa. Surface area of the supratrochlear fossa generally greater than, and the fossa generally wider distally than, in *Spatula discors*. Surface area of supratrochlear fossa greater than in *A. c. carolinensis*. Shaft depth across the major and minor metacarpals greater than observed in the modern comparative taxa.

Measurements. See Table 1.

Remarks. Fragmentary anatine postcranial bones can be undiagnosable to species. This particular bone was previously attributed to *A. c. carolinensis* by Brodkorb & Mourer-Chauviré (1984), and I agree that that is the likely identification. However, the bone differs in at least minor ways from all comparative skeletons and I cannot exclude the possibility that it should be referred to *S. discors* or an extinct species.

TABLE 1. Measurements (mm) of the proximal end of the carpometacarpus in small North American taxa of Anatidae, in comparison with the Cumberland Bone Cave fossil CM 34027. Depth = shaft depth through major and minor metacarpals. Width = width of proximal end excluding os metacarpale alulare (measurement taken from the ventral surface of the bone).

Taxon	Specimen	Depth	Width
Fossil	CM 34027	4.8	5.0
Anas crecca carolinensis	USNM BIRDS 610632	4.0	4.8
	USNM BIRDS 610635	4.0	4.7
	USNM BIRDS 638839	3.5	4.5
Bucephala albeola	USNM BIRDS 492434	3.6	4.8
	USNM BIRDS 644552	3.3	4.7
	USNM BIRDS 632035	3.2	4.5
Oxyura jamaicensis	USNM BIRDS 492491	3.7	4.7
	USNM BIRDS 499639	3.9	4.6
	USNM BIRDS 623361	3.6	4.3
Spatula discors	USNM BIRDS 502641	4.2	4.8
	USNM BIRDS 502645	4.2	5.0
	USNM BIRDS 502643	4.0	5.0
	USNM BIRDS 562841	3.9	5.1

Galliformes

Phasianidae

Meleagridinae

***Meleagris* sp.** Linnaeus

Material. USNM PAL 641967, l humerus: proximal half missing the deltopectoral and bicipital crests and a portion of the shaft below the head, collected July 2002 (Fig 1C). The bone appears to be from a full adult.

USNM PAL 641969, l humerus: nearly complete shaft missing articular surfaces of both ends and the crista bicipitalis, collected October 8, 1999 (Fig. 1A). On the caudal surface of the shaft, near the distal end, there are four distinct circular perforations and several similar lesions that do not fully perforate the bone (Fig. 1A). These are likely to be carnivore tooth punctures, resulting from an act of predation or scavenging. They show no sign of healing so they likely occurred at the time of death or afterwards.

USNM PAL 641971, r carpometacarpus: severely abraded proximal end and the proximal 1/3 of the shaft, missing the minor metacarpal, collected October 8, 1999.

CM 34028, l coracoid: dorsal portion, reported by Brodkorb & Mourer-Chauviré (1984).

USNM PAL 641968, r femur: the shaft and the abraded head are preserved; collected October 8, 1999, by Trent Spielman. The bone is immature as indicated by pits and striations on the shaft.

Measurements. The following bone measurements correspond with measurements reported by Steadman (1980). I have repeated Steadman's letter designations and wording for ease of comparison with his extensive statistical tables. USNM PAL 641969, humerus measurement C (width of midshaft) 12.5, humerus measurement D (depth of midshaft) 10.4. USNM PAL 641971, carpometacarpus measurement B (proximal depth) 15.9, measurement C (length of metacarpal one) 10.3. USNM PAL 641968, femur measurement D (width of midshaft) 9.4, measurement E (depth of midshaft) 7.3.

Description. Bones of the genus *Meleagris* are distinguished by very large size in the context of Phasianidae. The bones listed above are assigned to *Meleagris* based on size and morphological agreement. The bone measurements from fossils can be compared with Steadman's summary statistics for approximately 70 specimens of modern

M. gallopavo. Measurements of humerus USNM PAL 641969 fall below the reported range for males of *M. gallopavo*. The width of midshaft of the humerus is near the mean for *M. gallopavo* females, whereas the depth of midshaft is 0.1 mm greater than the range for females. The proximal depth of the carpometacarpus, USNM PAL 641971, falls below the reported range for males and females of *M. gallopavo* by 0.8 mm, and its length of metacarpal one falls within the range for both male and female *M. gallopavo*. Measurements of the femur USNM PAL 641968, an immature bone, fall below the range for males of *M. gallopavo*. Its width of midshaft is within the range for females, and depth of midshaft is below the reported range for females by 0.8 mm. Published measurements for the coracoid, CM 34028, are within the range for females of *M. gallopavo*.

Remarks. The comparative osteology and fossil record of *Meleagris* have been extensively studied (e.g., Steadman 1980; Bocheński & Campbell 2006). The two extant species of *Meleagris* show few fixed osteological differences and considerable intra-specific variation, including pronounced sexual size dimorphism. Only Pleistocene sites with large numbers of *Meleagris* bones provide an adequate basis for taxonomic assessment taking into account variability. The detailed study by Bocheński & Campbell confirmed that the abundant bones from the Rancho La Brea tar pits (Los Angeles, California) can be diagnosed as a distinct species, *M. californica* (Miller 1909a), closely related to *M. gallopavo*. Steadman studied the Pleistocene fossil record before the Rancholabrean land mammal age, including larger samples from an Irvingtonian (Coleman 2A, University of Florida Vertebrate Fossil Locality SM001) and a late Blancan (Inglis 1A, University of California Vertebrate Fossil Locality CI001) site in Florida. The Irvingtonian turkeys tended to be larger than those from the late Blancan, and the late Blancan birds lacked a pneumatized scapula which is present in later time periods. Steadman considered it likely that one or more successive fossil species of *Meleagris* had a very broad distribution in North America (similar to that of modern *M. gallopavo*) and had geographically variable morphology during the Early and Middle Pleistocene. He posited that most known Blancan and Irvingtonian fossil turkeys represent archaic forms of *M. gallopavo*.

Steadman (1980) and Bocheński & Campbell (2006) both reported osteological character states that differ at least in prevalence among various named taxa and local fossil assemblages of *Meleagris*, but unfortunately, none of them can be observed in the fossils from Cumberland Bone Cave. Considering their lack of diagnostic species-level traits, I have refrained from assigning the fossils a species-level identification, while recognizing that the combined evidence of morphology and biogeography suggests that they represent an archaic form of *M. gallopavo,* as envisioned by Steadman. This small collection of mid-Pleistocene turkey bones provides no evidence to refute Steadman's finding that *Meleagris* in North America has increased in body size since the late Blancan.

Tetraoninae

Bonasa umbellus

Material. USNM PAL 641979, l tarsometatarsus: shaft lacking the trochleae and proximal articular surfaces, collected by Trent Spielman, probably on October 2, 1996 (Fig. 1I).

USNM PAL 769092, l tarsometatarsus: shaft lacking most of the plantar surface, collected by Trent Spielman in the 1990s.

Description. All of the fossils of Tetraoninae from Cumberland Bone Cave fall within or close to the size range of modern *B. umbellus*. Among New World Tetraoninae, *Bonasa umbellus* is much larger than *Lagopus leucura* but considerably smaller than all others except *Falcipennis canadensis, Lagopus lagopus*, and *L. muta*. *Bonasa* differs from *Lagopus* and *Falcipennis* in having a proportionately long and slender tarsometatarsus. The two tarsometatarsi listed above are referable to *B. umbellus* on that basis. Note that USNM PAL 641979 appears to be from a full adult and is large compared with some *B. umbellus* skeletons, but is a good match for USNM BIRDS 641459, a male from Alberta, Canada.

Remarks. See below.

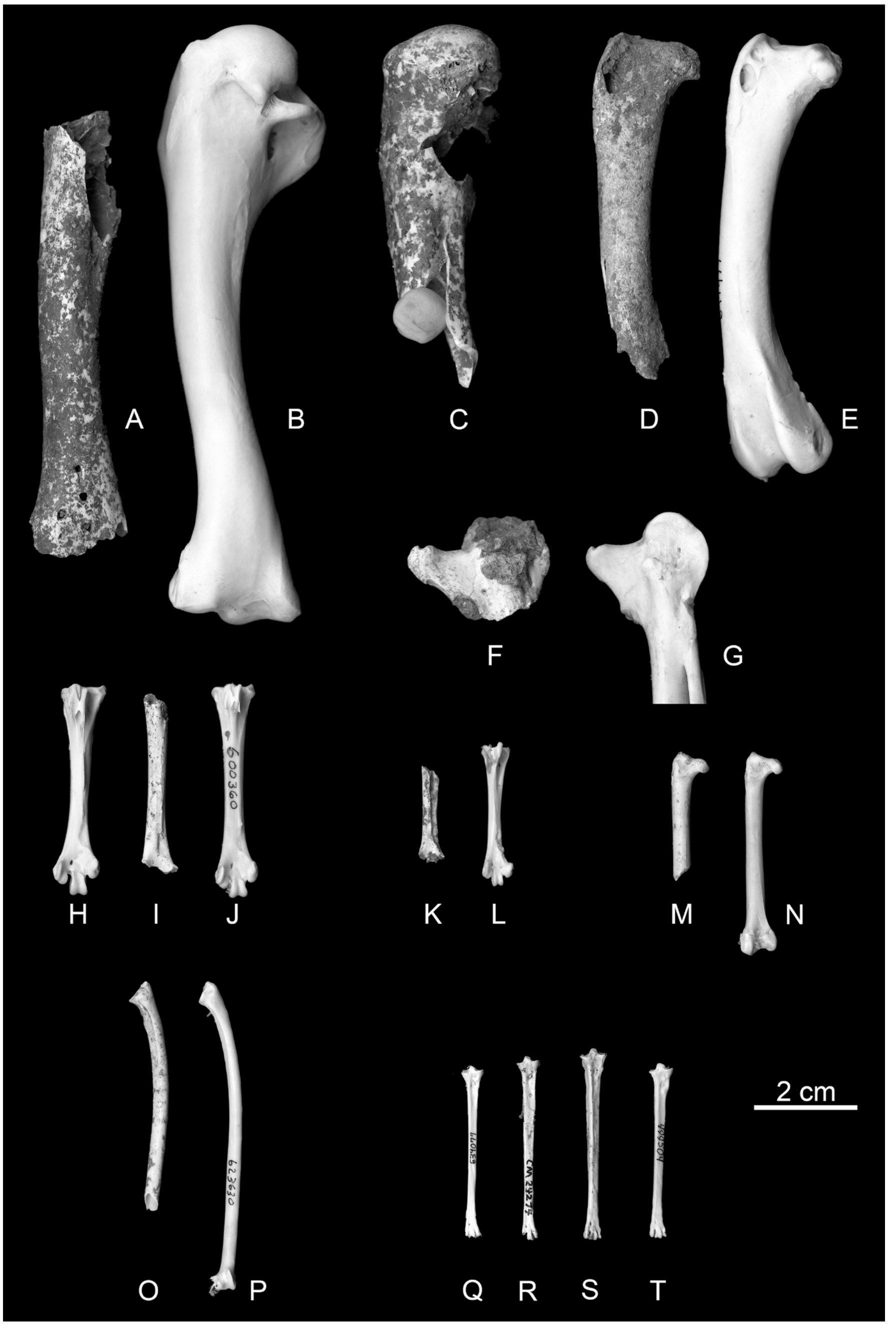

FIGURE 1. Fossils from Cumberland Bone Cave compared with modern taxa. A) fossil left humerus of *Meleagris* sp., USNM PAL 641969, caudal aspect; B) left humerus of *Meleagris gallopavo*, USNM BIRDS 556334 f, caudal aspect; C) fossil left humerus of *Meleagris* sp., USNM PAL 641067, caudal aspect; D) fossil right femur of *Coragyps atratus*, USNM PAL 641790, cranial aspect; E) right femur of *C. atratus*, USNM BIRDS 647499 m, cranial aspect; F) fossil proximal right carpometacarpus of fossil *Branta dickeyi*, USNM PAL 641972, ventral aspect; G) proximal right carpometacarpus of *B. canadensis*, USNM BIRDS 488182 m, ventral aspect; H) left tarsometatarsus of *Falcipennis canadensis*, USNM BIRDS 557527 f, plantar aspect; I) fossil left tarsometatarsus of *Bonasa umbellus*, USNM PAL 641979, plantar aspect; J) left tarsometatarsus of *B. umbellus*, USNM BIRDS 600360 f imm., plantar aspect; K) fossil left tarsometatarsus of *Ectopistes migratorius*, USNM PAL 769090, plantar aspect; L) tarsometatarsus of *E. migratorius*, USNM BIRDS 292904 (captive), plantar aspect; M) fossil left femur of *Megascops guildayi*, USNM PAL 769089, caudal aspect; N) left femur of *Megascops asio*, USNM 623630 f, caudal aspect; O) fossil right ulna of *M. guildayi*, USNM PAL 641984, ventral aspect; P) right ulna of *M. asio*, USNM BIRDS 623630 f, ventral aspect; Q) right tarsometatarsus of *Perisoreus canadensis*, USNM BIRDS 639077 f, dorsal aspect; R) fossil right tarsometatarsus of a species of jay (Corvidae, aff. *Perisoreus/Cyanocitta*), CM 24274, dorsal aspect; S) fossil right tarsometatarsus of a species of jay (Corvidae, aff. *Cyanocitta/Perisoreus*), USNM PAL 641989, dorsal aspect; T) right tarsometatarsus of *Cyanocitta cyanea*, USNM BIRDS 499504 f, dorsal aspect. Scale bar 1, for images A–G, = 2 cm. Scale bar 2, for images H–N, = 1 cm.

Tetraoninae sp.

Material and Descriptions. USNM PAL 641987, l coracoid: sternal half lacking the lateral process and with much of the dorsal surface of the bone damaged, collected in the 1990s. The bone agrees in morphological details with the four species under consideration but does not preserve enough morphological detail to allow for diagnosis at the species level. It is moderately larger than comparative skeletons of *B. umbellus*. The bone has been gnawed by a small mammal, likely a rodent.

USNM PAL 641975, l coracoid: shaft missing sternal end and part of processus acrocoracoideus, collected May 14, 1999. In galliforms, the ventral surface of the shaft typically has a blunt crest running from the acrocoracoid process nearly to the sternal end of the bone. The fossil differs from *L. lagopus, L. mutus*, and *F. canadensis*, and agrees with *B. umbellus*, in having this crest more prominent, so that the ventral surface attains a more acute angle. It differs from *B. umbellus* and *F. canadensis*, and agrees more with *Lagopus,* in having a wider facies articularis humeralis. This combination of attributes leaves the generic assignment of the bone uncertain.

USNM PAL 641976, l scapula: cranial one-third only, collected on October 8, 1999. The bone is immature, with its shaft heavily striated and articular surfaces pitted. It is smaller than comparative adult *Bonasa umbellus* skeletons.

USNM PAL 641974, l humerus: shaft only, preserving the proximal tip of the brachial depression, collected in the 1990s. The bone appears adult. The size of the bone and the stout, curvy shaft agree well with *B. umbellus* and *F. canadensis*.

USNM PAL 11690, l humerus: distal half, referred to *B. umbellus* by Wetmore (1927). A well-preserved specimen that agrees in fine detail with *B. umbellus* but also closely resembles *L. lagopus* and *F. canadensis.* In the comparative series examined, *B. umbellus* tends to have a more distinct olecranon fossa than the other two species. The fossil tends to agree with *B. umbellus* in this regard, but the trait is variable and is insufficient grounds for positive attribution.

USNM PAL 641988, abraded ulnare collected in the 1990s. An uncatalogued radiale, stored with this one and with the same provenience data, could well be the same species.

USNM PAL 769091, ulnare: complete, collected on May 14, 1999.

USNM PAL 641978, left carpometacarpus: proximal end only, collected by Trent Spielman probably on October 2, 1996 (illegible).

USNM PAL 641977, l femur: shaft only, collected in 2009. Agrees with *B. umbellus* and *F. canadensis* in having the caudal intramuscular lines less wide-set than in *Lagopus*. The shaft circumference is greater than in comparative skeletons of *B. umbellus* and *F. canadensis*, but still much smaller than in *Tympanuchus*.

Remarks. I have referred only two of the ten bones of Tetraoninae in the assemblage to *B. umbellus* and have left the rest unidentified to genus, including the distal humerus referred to the species by Wetmore (1927). As Steadman (2005) observed, postcranial skeletal elements of *B. umbellus* and *F. canadensis*, other than the tarsometatarsus, generally cannot be distinguished. However, I note that the other eight bones provide no clear evidence to refute the supposition that *B. umbellus* is the only species of Tetraoninae present. Note too that although I referred the two tarsometatarsi to the living species, it is possible that they instead represent a chronospecies of *B. umbellus* or an extinct species of *Bonasa*.

Cumberland Bone Cave provides the sole Irvingtonian fossil record of *B. umbellus* and the oldest fossil record of the genus and species. The species has been reported from late Pleistocene and Holocene sites in North America, particularly in the southeast (e.g., Brodkorb 1959; Wetmore 1962; Steadman 2005). *Bonasa umbellus* is the only extant species of grouse that occurs in the mid-latitude Appalachians or in the mixed hardwood forest habitat that is characteristic of the region at present (Rusch *et al.* 2000).

Cathartiformes

Cathartidae

Coragyps atratus

USNM PAL 641970, r femur: proximal end and most of the shaft, collected October 8, 1999 (Fig. 1D).

Description. The bone displays adult features including a distinct crista and fossa trochanteris, articular facet for the antitrochanter, and femoral head with the neck and the fovea ligamentum capitis developed, but it is clearly immature in that the exposed shaft is densely covered with short, fine striations, the fossa trochanteris is spongy, and the head retains dense, fine pores. It agrees remarkably in size, form and fine morphological details with *Coragyps atratus*, including the shaft curvature, proportions of the proximal end including the thick neck, the sharp and moderately elevated form of the crista trochanteris, and the proximal placement of the pneumatic foramen on the cranial surface. Larger than *Cathartes aura* and with the femur shaft distinctly bowed rather than straight as in that species. An immature individual of *H. leucocephalus* with similar bone surface textures (USNM BIRDS 611757 f) has a much longer femur (length from trochanter to the prominent nutrient foramen on the caudal aspect of the shaft, 57.7 mm in *H. leucocephalus* vs. 37.0 in the fossil) but is less advanced towards adult morphology (e.g., femoral head much less produced, crista trochanteris not distinct, no fossa trochanteris or fovea ligamentum capitis, articular facet for the antitrochanter bulbous). Likewise, the fossil is much smaller than the extant *Aquila chrysaetos*, and the adult features that the fossil has attained differ in form from the two eagles (crista trochanteris less elevated proximally above the proximal articular surface than in *H. leucocephalus*, more elevated and more distinct than in *A. chrysaetos*). *Amplibuteo concordatus* Emslie and Czaplewski 1999, an extinct eagle known from Blancan and early Irvingtonian sites in Florida, was not directly compared but is unlikely to be relevant due to its eagle-like rather than *Coragyps*-like osteology.

Measurements. Howard (1968) summarized measurements from a large series of *Coragyps occidentalis* (Miller 1909b) bones from the Rancho La Brea tar pits, of which only the least transverse breadth of the shaft (8.9 mm) can be observed in the Cumberland Bone Cave femur. For this measurement, Howard reported a mean of 9.1 mm in modern *C. atratus* and a minimum of 9.0 mm in 65 femora of *C. occidentalis*.

Remarks. The late Pleistocene (Rancholabrean) species *C. occidentalis,* is known from multiple localities in southwestern North America and is believed to have become extinct along with the Pleistocene megafauna (Brasso & Emslie 2006). Bones of this species are larger on average than in modern *C. atratus* (Howard 1962, 1968; Frailey 1972). Because the fossil femur has not attained adult surface textures, we cannot exclude the possibility that its full adult size would be above the range of modern *C. atratus* and within the range of the larger late Pleistocene species. It is notable that *C. atratus* has not moved into most of the southwestern range of *C. occidentalis* in the time since the extinction of the latter, roughly ten thousand years ago. This suggests that *C. occidentalis* occupied arid habitats that are not suitable for *C. atratus*.

The immature bone of *C. atratus* provides evidence that the species was breeding in or near the cave. We can rule out the possibility that the bird had flown from elsewhere to reach Cumberland Bone Cave by analogy with a growth series of California Condor (*G. californianus*) skeletons. The developmental stage of the fossil most closely matches that of a condor that died at 136 days old (USNM BIRDS 658188), in which the femur is likewise at or close to full adult size and form, has a finely striated shaft, dense pores on the femoral head, and the fossa trochanteris still spongy. The fossil femur is more advanced developmentally than a bird that died at 80 days old (USNM BIRDS 658191), which has not attained adult size and has the articular ends not fully formed or ossified. In two older condor chicks that died ten or fifteen days after the usual age of fledging (AMNH 32153, 184 days, and USNM BIRDS 658221, 187 days), the surface of the femoral shaft has attained the smooth surface texture and rugose topography seen in adult birds, although both femora retain some porous structure on the proximal articular surface.

The *G. californianus* skeleton with the femur at a similar stage of development to the fossil has a relatively underdeveloped forelimb, with the major wing bones still spongy and growing at the articular surfaces and the carpals and metacarpals unfused, and has the sternum still entirely porous and spongy (see USNM BIRDS 658188). It is no surprise, then, that California Condor chicks typically fledge at an older age (about 30 to 40 days older) than that of the individual that best matched the fossil (Snyder & Snyder 2000). Assuming the developmental pattern is similar in *Coragyps*, the fossil vulture from Cumberland Bone Cave would not yet have been able to fly.

Accipitriformes

Accipitridae

Accipitrinae

Aquila chrysaetos (Linnaeus)/*A. bivia* Emslie & Czaplewski 1999

Material. CM 34018, r ungual phalanx with tip and base missing.

Description. Corresponds in size and shape with the terminal phalanx of digits one (the hind toe) and two of an eagle. Brodkorb & Mourer-Chauviré (1984) referred it to *A. chrysaetos* rather than *H. leucocephalus* based on large overall size and more gentle distal tapering of the claw core (plantar view), implying a longer claw. Based on these criteria, I found it to be larger than all comparative specimens of *H. leucocephalus* and most comparative skeletons of *A. chrysaetos.* It agrees well in size and shape with one comparative skeleton of *A. chrysaetos* (USNM BIRDS 19724). However, the possibility that it belongs to the larger early Irvingtonian species *Aquila bivia* cannot be excluded.

Remarks. This large ungual phalanx appears to be attributable either to the Golden Eagle (*A. chrysaetos*) or to a larger, early Irvingtonian species of *Aquila* described from Florida and Arizona (Emslie & Czaplewski 1999). The modern distribution of the Golden Eagle in North America is primarily in the west, but the species does have a rarely observed wintering population in the region of Cumberland Bone Cave (Brodeur *et al.* 1996).

Accipiter cooperi

Material. USNM PAL 641980, l coracoid: dorsal one-third, collected October 8, 1999.

Description. The bone falls in the size range of large males and small females of modern *A. cooperi*. I compared it with modern species of North American Accipitriformes in roughly the same size class. The fossil is much more slender and less pneumatic than in *Elanoides forficatus* or *Rostrhamus sociabilis*. The pneumatic foramen in the sulcus m. supracoracoidei is smaller and the acrocoracoid process is less inflated than in *Circus cyaneus*. The fossil resembles *A. cooperi* as opposed to *Buteo lineatus* and *B. platypterus* in having a relatively slender facies articularis humeralis (glenoid facet) and a less extended procoracoid process.

Remarks. This species still occurs in the region of the cave. It was previously reported from other Irvingtonian fossil localities and from a late Blancan locality in Florida (Emslie 1998).

Accipitridae, aff. *Accipiter cooperi*

Material. USNM PAL 641996, pedal phalanx, entire, with the articular cotyla slightly crushed; collected in the 1990s.

USNM PAL 641983, ungual phalanx, entire; collected Sept 22, 1994.

Description. Neither bone is diagnosable at the species level but both compare well with *A. cooperi* in size and shape.

Remarks. See above.

Haliaeetus leucocephalus

Material. USNM PAL 641982, ungual phalanx: proximal 1/3, collected July 2002.

Description. Agrees in size with the third or fourth ungual phalanx in *H. leucocephalus* and *A. chrysaetos*. Its small size and narrow articular cotyla suggest it is from the fourth digit. Although there is morphological overlap between the two species in this element, the fossil can be assigned to *H. leucocephalus* as opposed to *A. chrysaetos* based on the following combination of traits: articular cotyla narrower (proximal view) and with a tighter curve (lateral view), flexor tubercle bulbous and distended as opposed to crested and elongated.

Remarks. The assignment of this fossil to *H. leucocephalus* is based on morphological agreement but it comes with the caveat that comparisons with the Plio-Pleistocene fossil eagle from Florida and Arizona, *Amplibuteo concordatus* Emslie & Czaplewski 1999, were not possible. However, based on the published measurements of its long bones, *A. concordatus* was smaller in body size than *H. leucocephalus* or *A. chrysaetos*. *Haliaeetus leucocephalus* currently occurs in the region of the cave.

Columbiformes

Columbidae

Ectopistes migratorius

Material. CM 34020, r coracoid: cranial portion lacking procoracoid process, referred to *E. migratorius* by Brodkorb & Mourer-Chauviré (1984). Not reexamined for this study.

USNM PAL 769090, l tarsometatarsus: shaft missing the proximal end and the trochleae, collected Sept 22, 1994 (Fig. 1K).

Description. The tarsometatarsus is much larger than in *Zenaida* and closer in size to those of males of *Patagioenas fasciata*. Proportionately long and slender compared with *P. fasciata*, *P. leucocephala*, and *P. cayanensis*. The median crest on the plantar surface increases in depth as it extends proximally to join the hypotarsus in *Patagioenas* but is shallower along its full length in the fossil. The fossil shares a shallow median crest with those of *Ectopistes* and *Zenaida*. This crest is less deep proximally in *P. leucocephala* than in the other *Patagioenas*, but still more deep than in *Ecotopistes* and the fossil. Only two of the five comparative skeletons of *Ectopistes* include the tarsometatarsus, and in both cases the bone is distinctly smaller than the fossil. Three additional partial comparative skeletons are known to be males, and these three have considerably larger skeletons, suggesting that the fossil is within the size range of male *Ectopistes*.

Remarks. The Cumberland Bone Cave bones referred to *E. migratorius* appear to be the oldest documented fossil record of the species, which is also known from late Pleistocene (Rancholabrean) sites including some western localities outside the species' historical range (Hargrave & Emslie 1980; Chandler 1982). The cave locality falls within the primary breeding range of the species during the 19th century (Blockstein 2002).

cf. *Ectopistes migratorius*

Material. USNM PAL 641973, r coracoid, cranial half missing part of the acrocoracoid process, collected Sept. 22, 1994.

Description. Agrees in size and morphological detail with a male comparative skeleton of *E. migratorius* (USNM BIRDS 224320), including in having a slender procoracoid process.

Remarks. See above.

Strigiformes

Strigidae

Megascops guildayi (Brodkorb and Mourer-Chauviré 1984)

Material. USNM PAL 641984, r ulna: shaft and proximal end, collected in 1991 (Fig. 1O).

USNM PAL 641985, r ulna: distal articular end only, collected October 2, 1996.

USNM PAL 769089, l femur: proximal 2/3, collected Sept. 22, 1994 (Fig. 1M).

CM 8040 holotype, l tarsometatarsus lacking proximal end. Not reexamined for this study.

USNM PAL 769088, pedal phalanx: entire, collected Sept. 22, 1994.

USNM PAL 641981, ungual phalanx: entire, collected Sept. 22, 1994.

Description. The bones of a strigid owl listed above are referred to *M. guildayi* based primarily on the criteria of size (smaller than *Asio otus*, larger than *Megascops asio* and *M. kennicottii*) and agreement in morphological details with modern *Megascops*. The proximal half of the ulna agrees with those of *Megascops*, *Athene*, and *Aegolius* in being more curved than in *Asio*, *Strix*, or *Surnia*. The proximal articular surfaces of the femur are broader in relationship to depth than in *Athene* or *Aegolius*, agreeing in this trait with *Megascops* and larger owls. No complete long bones of the species are known, and the larger size of the fossil species compared with other *Megascops* is evident mainly from the thicker shafts of the ulna and femur. The tarsometatarsus, described and figured by Brodkorb & Mourer-Chauviré (1984: Figure 1), is referable to *Megascops* based on size and narrow, slender form, though proportionately stouter and shorter than in *Athene cunicularia*. The tarsometatarsus is not as stout as in *Asio brevipes* Ford & Murray 1967 from the Upper Pliocene of Idaho nor as slender as in *Athene megalospeza* (Ford 1966) from the Upper Pliocene of Kansas and Idaho.

Measurements. USNM PAL 641984 (ulna), greatest width distal to cotylae, 5.2 mm. USNM PAL 769089 (femur), proximal lateromedial width from head through trochanter, 7.0 mm; width of head, 3.3 mm.

Remarks. The only previously known material of this species is the type specimen. The new material bolsters the evidence for a large extinct species of *Megascops* in the Irvingtonian of Maryland. It is odd that the species has no other fossil record, but perhaps some of the Pliocene fossils referred to *Otus* (=*Megascops*) are relevant to it (i.e., two bones from the Hagerman local fauna of Idaho (Ford & Murray 1967) and one from the Rexroad Formation of Kansas (Ford 1966)).

Strigidae sp.

Material. USNM PAL 641986, r femur: distal end only, collected May 14, 1999.

Description. Smaller than, and with the fibular trochlea wider than in, *Tyto alba*. Among extant North American owls, closest to *Asio otus* and males of *Surnia ulula* in size. Differs from *S. ulula* and agrees with *A. otus* in having the medial condyle less bulbous and projecting less far mediad, the popliteal fossa and the intercondylar sulcus shallower, and the juncture of the tibiofibular crest with the shaft forming a tight curve as opposed to a shallow slope.

Measurements. The maximum distal breadth in the fossil (8.4 mm) falls just below the range reported by Emslie (1982) for *A. otus* (8.5-10.2 mm, n=10).

Remarks. The fossil compares favorably with *Asio*, however, the possibility that it represents a large female of *Megascops guildayi* cannot be ruled out. I consider the bone to be undiagnostic at the level of the genus.

Passeriformes

Tyrannidae

Tyrannidae sp.

Material. USNM PAL 641993, r tarsometatarsus: distal extremity lacking trochlea metatarsi IV, with shaft extending to just proximal of fossa metatarsi I, collected in the 1990s. The bone appears fully adult.

Description. The fossil closely resembles but is somewhat more gracile than *Sayornis phoebe*. I consider it to be undiagnostic at the genus and species level.

Corvidae

Corvidae, aff. *Cyanocitta/Perisoreus*

Material. CM 24274, r tarsometatarsus with damage to the hypotarsus and repair to the shaft (Fig. 1Q). Referred to *Perisoreus canadensis* by Brodkorb & Mourer-Chauviré (1984).

USNM PAL 641989, r tarsometatarsus: entire, collected in the 1990s (Fig 1s). A break mid-shaft has been repaired.

USNM PAL 641990, l tarsometatarsus: distal three-fourths, collected July 2002.

USNM PAL 641991, r tibiotarsus: distal half, collected Sept. 22, 1994.

USNM PAL 641994, l carpometacarpus lacking proximal end, collected July 2002.

Description. These five passerine bones are recognizable as New World jays, family Corvidae, based on size and morphological agreement. They represent either a single species or multiple species of similar size. They cannot be assigned to any of several fossil species of North American jays of late Blancan and Irvingtonian ages (*Protocitta dixi* Brodkorb 1957, *Protocitta ajax* Brodkorb 1972, *Henocitta brodkorbi* Holman 1959), which are considerably larger in body size. One of the fossil tarsometatarsi (CM 24274) has a particularly narrow shaft distally, and the tibiotarsus also has a narrow distal shaft in relationship to condyle breadth. These traits are not diagnostic to species according to the morphometric analysis described below.

Measurements. See Appendix 1 and Figures 2-4.

Morphometric Analysis. I used a morphometric approach to compare the fossils with modern species of jays from continental North America north of Mexico (Canada Jay *P. canadensis*, Blue Jay *Cyanocitta cristata*, three species of scrub jays, *Aphelocoma coerulescens*, *woodhouseii*, and *californica*, and the larger Steller's Jay *Cyanocitta stelleri*). Bone lengths could only be taken from the fossil carpometacarpus and the two tarsometatarsi. Boxplots for these measurements illustrate differences in intermembral proportions among the taxa, with *Aphelocoma* having a long tarsometatarsus relative to carpometacarpus, and *Perisoreus* and even more so *Cyanocitta cristata* having a short tarsometatarsus relative to carpometacarpus (Fig. 2). For the fossils, even with the small sample size, it can be seen that if only one species of jay is present, its body proportions are not consistent with assignment to *Aphelocoma*. The fossil tarsometatarsi are also distinctly smaller than in *C. stelleri*.

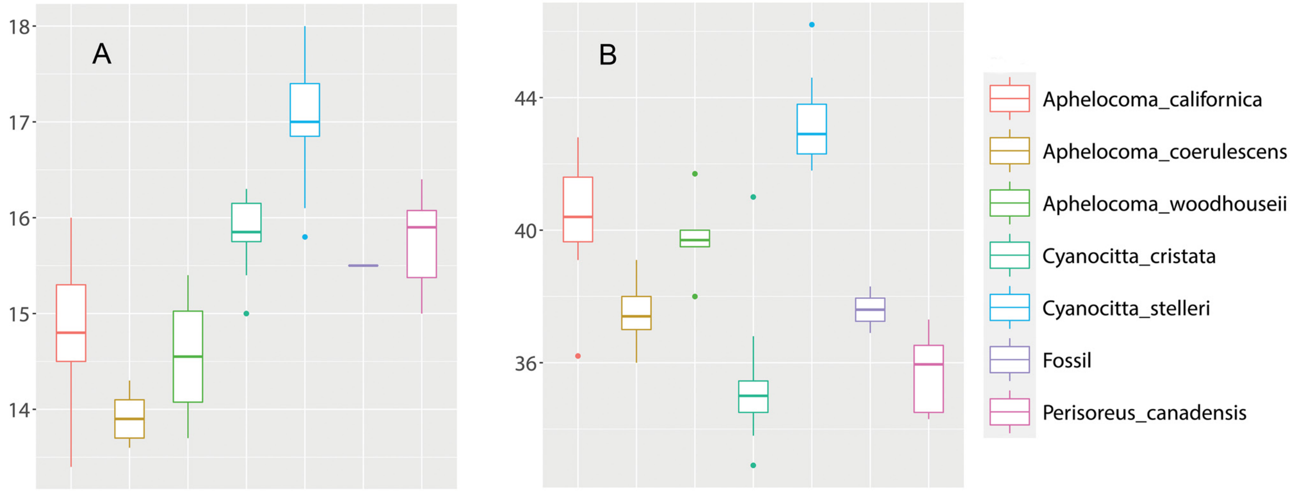

FIGURE 2. Box and whisker plots summarizing long bone lengths in North American jays. A) Carpometacarpus, length of major metacarpal (mm); B) tarsometatarsus length (mm). Data from Appendix 1.

To evaluate the fossil tibiotarsus, width of the distal shaft and width across the distal condyles were taken. The ratio of these measurements shows that the fossil tibiotarsus has an unusually slender shaft (Fig. 3). It agrees with *P. canadensis* in this trait although it is also within the range of *A. woodhouseii*.

Brodkorb & Mourer-Chauviré (1984) referred the tarsometatarsus CM 24274 to *P. canadensis* based on its slender shaft. To evaluate the intramembral proportions of the two fossil tarsometatarsi, I measured tarsometatarsus length and four width measurements covering proximal and distal articular and shaft widths (Appendix 1). I performed a principal components analysis using four variables: 1) length from intercotylar area to the trochlea of the third metatarsal, 2) proximal width across articular facets, 3) proximal shaft width at level of proximal vascular foramina, 4) distal shaft width at level of distal vascular foramen (Fig. 4). I also ran this analysis with five variables (distal width across trochleae included), with very similar results (not shown). In the four-variable analysis, for the first principal component, the variables' loadings had the same sign and a moderate range of values (variable 1 = -0.52, variable 2 = -0.55, variable 3 = -0.49, variable 4 = -0.44). This component, weighted most heavily on length and the proximal widths, reflects size and also some shape variance, as clearly shown by the reversal of the positions of *C. cristata* and *P. canadensis* relative to their tarsometatarsus lengths (compare Figs. 2b and 4). The second principal component contrasted tarsometatarsus distal shaft width (component loading -0.80) with proximal shaft width (loading +0.48) and total length (loading +0.33). This component tended to distinguish *A. californica* and *A. woodhouseii* from the other taxa but otherwise was ineffective at separating the species. The two Cumberland Bone Cave fossils are centrally placed in the principal components biplot (Fig. 4). CM 24274 falls just outside the probability ellipse for *P. canadensis*, which supports Brodkorb & Mourer-Chauviré's opinion of the bone; however, it also falls within the probability ellipse for *C. cristata* and just outside the ellipses of the three species of *Aphelo-*

coma. USNM PAL 641989 falls near the center of the plot, within the ellipses for *C. cristata* and *A. coerulescens*. Considering that these are merely 68% probability ellipses, representing one standard deviation, I conclude that the tarsometatarsus data are indecisive with regard to the genus or species of jay(s) represented.

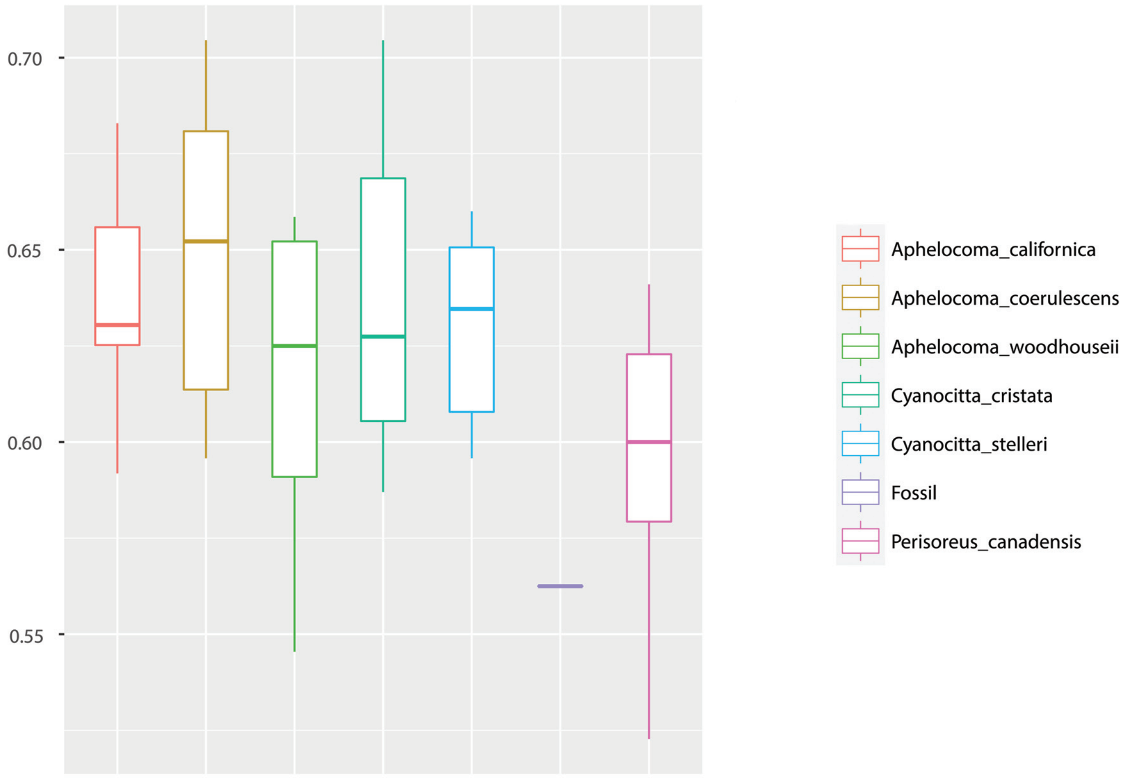

FIGURE 3. Box and whisker plot summarizing the ratio of shaft width to distal condylar width in North American jays. Data from Appendix 1.

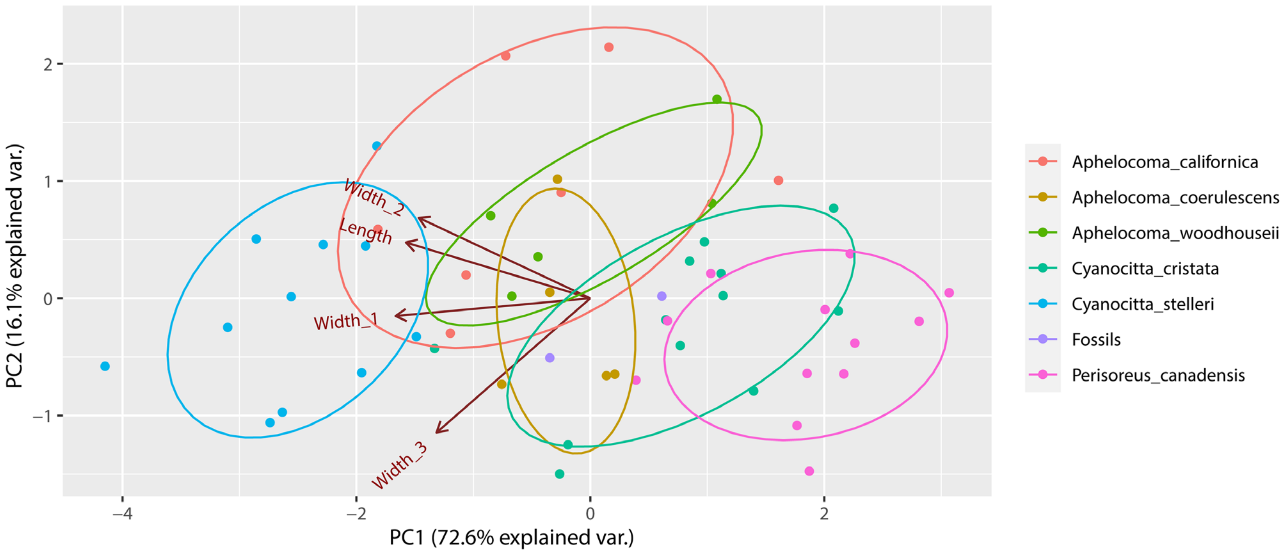

FIGURE 4. Plot of the first two principal components for tarsometatarsus dimensions in North American jays. Data from Appendix 1.

Remarks. The fossil jays received extra scrutiny because Brodkorb & Mourer-Chauviré cited their identification of *P. canadensis* as evidence that the Cumberland Bone Cave assemblage accumulated during a cold climate phase. Although the osteometric analysis eliminated *C. stelleri* on size and provisionally eliminated *Aphelocoma* on body proportions (assuming only one species is represented by the fossils), it was otherwise indecisive as to the genus and species represented. *Perisoreus canadensis* has also been reported as a fossil in another southerly location, Cheek Bend Cave in Tennessee (Parmalee & Klippel 1982). The bird and mammal assemblage from Cheek Bend Cave includes a number of boreal species and was interpreted as dating to the Last Glacial Maximum. In the case of Cumberland Bone Cave, *Perisoreus*, if present, would be the only purely boreal element in the avian assemblage (see Discussion).

Passerellidae

Passerellidae sp.

Material. USNM PAL 641992, l mandibular ramus lacking symphyseal part and medial process. Collected Oct. 7, 1998.

Description. Similar to but somewhat larger than in *Junco hyemalis* and somewhat smaller than in *Zonotrichia albicollis*.

Fringillidae/Cardinalidae

Indeterminate Finch

Material. USNM PAL 641995, l quadrate lacking orbital process. Collected in the 1990s.

Description. Agrees in general form with species in the Fringillidae and Cardinalidae that have finch-like bill shapes. The limited extent of pneumatization of the caudal surface of the otic process suggests that the quadrate is assignable to Fringillidae not Cardinalidae. In size, it is somewhat smaller than *Cardinalis cardinalis*.

Discussion

North American birdlife during the Irvingtonian land mammal age is best known from the southern Rocky Mountains (Porcupine Cave, Emslie 2004) and from several localities in peninsular Florida (Emslie 1995, 1998). The assemblage from Cumberland Bone Cave comprises at least 14 species (Table 2) and helps to fill the geographic gaps in distribution of avian fossils from this time period. The ecological types represented as fossils include ground-feeding birds (a turkey, the Ruffed Grouse, the Passenger Pigeon), a scavenger (Black Vulture), a number of raptorial species (Bald Eagle, Coopers Hawk, Golden Eagle or a close relative, a species of screech owl), a few aquatic species (a large goose, a small duck), and several perching birds (a flycatcher, a jay, a junco or sparrow, and a finch). Immature bones in the assemblage document breeding records for turkeys, grouse, and the Black Vulture. The fossils include new anatomical parts for the large extinct screech owl that is known only from this locality and appear to provide the oldest fossil record of Passenger Pigeon, extending the age range of the species to the mid-Pleistocene, approximately 700 to 800 kya. The large goose, *B. dickeyi,* has a broad geographic and long temporal distribution, as it is now reported from the Blancan of Oregon, the early Irvingtonian of Florida, the Irvingtonian of Maryland, and the Rancholabrean of California (although see the species account for a caveat about this poorly known species).

The proportion of extinct species in the avifauna is 20% or higher (minimally, *Branta dickeyi, Ectopistes migratorius*, and *Megascops guildayi*, plus there is uncertainty about several other taxa such as *Meleagris* sp. and *Aquila chrysaetos/bivia*). Whether any of these represent extinctions of a phyletic lineage by the end of the Irvingtonian is debatable. The Passenger Pigeon became extinct only a little more than a century ago. *Branta dickeyi* may represent the extinction of a phyletic lineage, but it's taxonomic status is uncertain and its fossil record extends into the Rancholabrean. In his comprehensive study of Blancan and Irvingtonian fossil turkeys, Steadman (1980) concluded that the modern Wild Turkey is a lineal descendant of fossil turkeys that have been geographically widespread in North America since Blancan and Irvingtonian times. Similarly, Brodkorb and Mourer-Chauviré (1984) considered it likely that their new species *M. guildayi* represents a larger Pleistocene form of the Eastern Screech Owl, *M. asio*, rather than an extinct lineage. From this perspective, it is possible to interpret the avifauna of the cave as containing no phyletic extinctions that were restricted to the Irvingtonian.

TABLE 2. Taxonomic list of birds identified in the Cumberland Bone Cave Local Fauna. NISP, Number of Identified Specimens.

Taxon	Common Name or Informal Description	**NISP**
Anatidae		
Branta dickeyi	large extinct goose	1
Anatinae, aff. *Anas crecca carolinensis*/*Spatula discors*	similar to Green- or Blue-winged Teal	1
Phasianidae		
Meleagris sp.	turkey	5
Bonasa umbellus	Ruffed Grouse	2
Tetraoninae sp.	similar to Ruffed Grouse	9
Cathartidae		
Coragyps atratus	Turkey Vulture	1
Accipitridae		
Aquila chrysaetos/bivia	Golden Eagle or larger extinct eagle	1
Accipiter cooperi	Cooper's Hawk	1
Accipitridae, aff. *Accipiter cooperi*	similar to Cooper's Hawk	2
Haliaeetus leucocephalus	Bald Eagle	1
Columbidae		
Ectopistes migratorius	Passenger Pigeon	2
cf. *Ectopistes migratorius*	similar to Passenger Pigeon	1
Strigidae		
Megascops guildayi	large extinct screech owl	6
Strigidae sp.	Medium-sized owl	1
Tyrannidae		
Tyrannidae sp.	similar to Eastern Phoebe	1
Corvidae		
Corvidae, aff. *Cyanocitta/Perisoreus*	similar to Blue or Canada Jay	5
Passerellidae		
Passerellidae sp.	a junco or sparrow	1
Fringillidae or Cardinalidae		
Fringillidae/Cardinalidae sp.	a finch	1
	SUM	42

For the sake of paleoecological interpretation, it was important to scrutinize the five bones attributable to New World jays because one of them was previously identified as a northern boreal and alpine species, the Canada Jay. This brought disharmony into the faunal list, considering that the modern distributions of Canada Jay and the Black Vulture are non-overlapping. The Black Vulture fossil from Cumberland Bone Cave occurs near the northern limit of the species' current breeding range (Buckley 1999), and the species historically had an even more southerly distribution, with the first breeding record in Maryland not occurring until 1922 (Robbins & Blom 1996). Canada Jays have a northern boreal distribution in the eastern half of North America and extend farther south only in western montane regions (Strickland & Ouellet 2018). Modern Wild Turkeys, Coopers Hawks, and screech owls also have essentially non-overlapping ranges with the Canada Jay if both geographic distribution and habitat type are taken into account. Considering that my osteometric analysis of the jay fossils neither confirmed nor excluded the presence of Canada Jay in the avifauna, the most parsimonious interpretation is that the species was absent. Under this assumption, there are no purely boreal elements in the Cumberland Bone Cave avifauna.

Setting aside the Canada Jay, all of the extant or potentially extant species identified still occur in the region of the cave today (as would the Passenger Pigeon if not forced into extinction). The avifauna thus paints a picture of only modest avifaunal turnover between the mid-Pleistocene and the late Holocene in the mid-latitude Appalachians. This is not to say that habitats were the same, especially considering the importance of human-modified habitats to modern populations of species like the Wild Turkey, Black Vulture, and Cooper's Hawk.

To gain insight into Irvingtonian habitats, it is worth considering the habitats used by modern counterparts of the fossil taxa. Canada Geese make use of diverse habitats, from lakes and rivers to marshes, meadows, and agricultural and urban habitats. They are not a woodland species except in the presence of wetlands, lakes, or rivers. Wild Turkey use a wide variety of mixed woodlands and grassy savannah habitats across their extensive range in North America. They use trees for roosting and fruit, seed, and mast for food. Hardwoods are often an important forest component in their habitat, and the presence of some more open habitat such as small pastures is preferred, especially for breeding. They are absent from high mountain regions and part of the Great Plains, and barely extend northward into Canada. Ruffed Grouse have a largely boreal distribution but descend to Tennessee in the Appalachians; they are year-round residents over most of their range. Aspen woodlands and boreal forest are primary habitat types but in the southeastern part of their range they associate with mixed deciduous-coniferous forest (oaks, hickories, pines). Males seek logs or other prominences for drumming, preferably located in protected understory clearings in early successional forest (Rusch *et al.* 2000). Black Vultures often seek the protection of forest for nesting and roosting; their distribution in forest tends to be riverine. They frequently lay their eggs on the ground in crevices or cavities (Robbins & Blom 1996), which may explain the presence of an unfledged chick in the cave site. As visual foragers, Black Vultures prefer to forage in more open habitat, and they require large home ranges during breeding (Coleman & Fraser 1989). Bald Eagles favor larger rivers, lakes, and shorelines but also occur along smaller rivers, including in the region of the cave locality. They prefer large trees near water for nesting and roosting but will nest on the ground if trees are absent. Golden Eagles are primarily birds of open habitat across their cosmopolitan distribution; however, birds that breed near Hudson Bay have been found to secretively over-winter in montane forest in the mid-latitude Appalachians, not far from the cave site. Cooper's Hawks are broadly distributed in deciduous, mixed, and coniferous forest and in small woodlots in North America. They tend to forage in wooded habitats more than open ones. Passenger Pigeons fed primarily on mast of beeches, oaks, and to a lesser extent, chestnuts, as well as grain and fruit. They required large expanses of forest for feeding. Most species of screech owls are neotropical; the two species with mainly temperate distributions occur in a tremendous variety of treed habitats but most commonly in riverine forest. They generally avoid high montane regions, and when they do enter these regions, they are often restricted to valley bottoms.

Taken together, these observations suggest that in the mid-Pleistocene, roughly 700 to 800 kya, habitat near Cumberland Bone Cave included mixed forest with mast-producing deciduous hardwoods like beeches and oaks. Both early and later successional stages were probably represented. A nearby river, lake or wetland would have provided habitat for Canada Goose, Bald Eagle, a screech owl and a small duck. Wills Creek currently provides such habitat near the site, and the North Branch of the Potomac River is close enough for eagle foraging. There are no clear boreal elements in the avifauna, and the habitats near the cave may not have differed greatly from those of the late Holocene. The exception may be that the region surrounding the cave apparently included enough open habitat for Black Vulture foraging during the breeding season, well before human influence.

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APPENDIX 1. Measurements (mm) of North American jays (Corvidae) in comparison with the Cumberland Bone Cave fossils. 1) Carpometacarpus, dorsal aspect, length of minor metacarpal from point just distal to facies articularis ulnocarpalis to distal end. 2) Tibiotarsus, cranial aspect, greatest width across condyles. 3) Tibiotarsus, cranial aspect, width of shaft across pons supratendineus. 4) Tarsometatarsus length from intercotylar area to trochlea metatarsi III. 5) Tarsometatarsus, proximal width across articular facets. 6) Tarsometatarsus, proximal shaft width at level of foramina vascularia proximalia. 7) Tarsometatarsus, distal shaft width at level of foramen vasculare distale. 8) Tarsometatarsus, width across trochleae.

			Measurement (mm)							
Species	**Catalog Number**	**Sex**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Fossils	CM 24274					36.9	4.8	2.8	2.5	
	USNM PAL 641989					38.3	5.3	2.7	2.6	3.4
	USNM PAL 641990								2.7	3.5
	USNM PAL 641991			4.8	2.7					
	USNM PAL 641994		15.5							
Aphelocoma californica	USNM BIRDS 611085	f	16	5	3.1	42.2	5.4	3.2	2.6	3.8
	USNM BIRDS 556692	f	13.4	4.1	2.8	36.2	4.4	2.9	2.3	3.2
	USNM BIRDS 641219	f	14.9	4.6	2.9	39.1	5	3.2	2.8	3.2
	USNM BIRDS 489825	m	14.8	4.6	3	42.8	4.9	3.3	2.3	3.3
	USNM BIRDS 556687	m	15.7	4.9	2.9	41	5	2.9	2.4	3.4
	USNM BIRDS 556689	m	14.5	4.7	3.1	40.4	4.9	3.2	2.7	3.5
	USNM BIRDS 556691	m	14.5	4.6	2.9	40.2	4.8	3.2	2.2	3.3
Aphelocoma coerulescens	USNM BIRDS 560527	f	13.9	4.4	3.1	38	4.7	3.4	2.5	3.3
	USNM BIRDS 611083	m	14.3	4.7	2.8	39.1	5	2.9	2.8	3.6
	USNM BIRDS 489957	m	13.7	4.6	3	37	5	3.1	2.6	3.6
	USNM BIRDS 611082	m	13.6	4.7	3.2	36	4.8	2.9	2.7	3.5
	USNM BIRDS 611081	m	14.1	4.4	2.7	37.4	4.8	2.8	2.7	3.3
Aphelocoma woodhouseii	USNM BIRDS 555357	f	13.7	4.1	2.7	38	4.6	3	2.2	3
	USNM BIRDS 346480	f		4.4	2.4	39.5	4.8	3.1	2.6	3.2
	USNM BIRDS 611086	f	14.9	4.4	2.6	40	4.7	2.6	2.3	3.2
	USNM BIRDS 614433	m	14.2	4.6	3	39.7	4.8	3.1	2.7	3.3
	USNM BIRDS 611084	m	15.4	4.8	3	41.7	5.1	3	2.5	3.3
Cyanocitta cristata	USNM BIRDS 614422	f	16.3	4.9	2.9	41	5.1	3	2.8	3.5
	USNM BIRDS 556922	f	15.4	4.4	3.1	33.8	4.6	2.7	2.6	3.3
	USNM BIRDS 15486	f	15.9	4.7	2.9	35.1	4.8	2.8	2.4	3.2
	USNM BIRDS 553644	f	15.8	4.5	3	33.9	4.7	2.7	2.2	3.5
	USNM BIRDS 554885	f	15	4.3	2.9	32.9	4.5	2.7	2.4	3.2
	USNM BIRDS 614425	f	15.8	4.5	2.8	34.7	4.7	2.9	2.6	3.5
	USNM BIRDS 499199	m	15.8	4.6	2.8	34.9	4.9	2.9	2.4	3.4
	USNM BIRDS 244063	m	16.3	4.5	3	35.9	4.7	2.9	2.4	3.2
	USNM BIRDS 612793	m	15.9	4.4	3	35.3	4.8	3	2.9	3.5

......continued on the next page

APPENDIX 1. (Continued)

			Measurement (mm)							
Species	**Catalog Number**	**Sex**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
	USNM BIRDS 614429	m	15.6	4.9	3.1	34.9	5	2.9	2.9	3.7
	USNM BIRDS 501365	m	16.3	4.6	2.7	35.1	4.9	2.7	2.4	3.2
	USNM BIRDS 554017	m	16.1	4.7	2.8	36.8	4.9	2.7	2.5	3.5
Cyanocitta stelleri	USNM BIRDS 557597	?	17.5	5.1	3.1	43.9	5.5	3.2	2.8	3.9
	USNM BIRDS 639067	f	17.5	5.2	3.4	42.9	5.7	3	3	3.9
	USNM BIRDS 614423	f	16.9	4.9	3.2	43.2	5.4	3.3	2.7	3.7
	USNM BIRDS 621170	f	18	5.6	3.5	46.2	5.9	3.4	3.1	4.2
	USNM BIRDS 554249	f	16.1	5	3	42.5	5.2	3.3	2.7	3.5
	USNM BIRDS 614412	f	17	5.1	3.1	42.7	5.3	3.4	2.5	3.5
	USNM BIRDS 637677	m	17.3	5	3.3	43.7	5.7	3.3	2.9	3.7
	USNM BIRDS 614420	m	16.8	4.7	2.8	42.1	5.1	3	2.8	3.5
	USNM BIRDS 634952	m	15.8	5.3	3.4	42	5.6	3.1	3	3.6
	USNM BIRDS 554248	m	16.9	5.4	3.5	44.6	5.7	3.3	2.7	3.4
	USNM BIRDS 611073	m	17	5.2	3.3	41.8	5.6	2.9	2.8	3.7
Perisoreus canadensis	USNM BIRDS 622673	f	15.4	4.4	2.3	34.3	4.7	2.3	2.6	3
	USNM BIRDS 638977	f	15.3	4.1	2.3	34.3	4.4	2.5	2.5	3.1
	USNM BIRDS 611071	f	15.9	3.9	2.5	34.5	4.2	2.4	2.3	2.9
	USNM BIRDS 489636	f	15.2	4.1	2.6	35.6	4.5	2.4	2.6	3.1
	USNM BIRDS 622714	f	15.9	4.2	2.6	36.5	4.4	2.5	2.3	3.1
	USNM BIRDS 622715	f	15	4.1	2.6	34.5	4.5	2.6	2.4	3.2
	USNM BIRDS 489629	f	15.5	4	2.4	35.1	4.5	2.4	2.4	3
	USNM BIRDS 489846	m	16.4	4	2.2	36.4	4.4	2.2	2.3	3
	USNM BIRDS 613826	m	16.3	4.1	2.4	36.3	4.5	2.4	2.5	3.2
	USNM BIRDS 639078	m	16	4.5	2.7	36.7	4.9	2.7	2.5	3.3
	USNM BIRDS 639078	m	15.9	4.4	2.7	36.6	4.8	2.7	2.4	3.3
	USNM BIRDS 489632	m	16.4	4.7	2.8	37.3	5	2.6	2.6	3.4