

Biodiversity Response to Climate Change in the Middle Pleistocene

The Porcupine Cave Fauna from Colorado

Edited by

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The Early and Middle Pleistocene Avifauna from Porcupine Cave

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Porcupine Cave is a multiroom limestone cave located in the southern Rocky Mountains of Park County, central Colorado, at an elevation of 2900 m. The cave was sealed for millennia until mining operations created an entrance in the late 1800s. Paleontological excavations, initiated by the Carnegie Museum of Natural History in 1986, were continued by the Denver Museum of Nature and Science. These excavations produced a rich collection of fossil vertebrates ranging in age from the early to the middle Pleistocene. Only fossils of the Carnivora and some of the rodent fauna have been reported previously (Barnosky and Rasmussen, 1988; Wood and Barnosky, 1994; Anderson, 1996; Barnosky et al., 1996; Bell and Barnosky, 2000).

Although mammalian remains dominate the vertebrate fauna, nearly 200 avian fossils were also recovered from the deposits. This avifauna is reported here and represents at least 45 taxa, the richest and most diverse assemblage of this age known from the intermountain western United States. Analysis of this avifauna provides new information on the composition of high-elevation avian communities in the early to middle Pleistocene in this region.

Materials and Methods

All fossil specimens were identified using comparative osteological collections at the U.S. National Museum, Washington, D.C., and the Florida Museum of Natural History (FLMNH), Gainesville. Terminology follows that of Howard (1929), and systematic presentation and taxonomy follow that of the American Ornithologists' Union (1998, 2000). Common names of most species mentioned below are noted in tables 10.1–10.13 and 12.1. Common names of birds not appearing in those tables are noted parenthetically after the first mention of the scientific name in the text. All fossil specimens are housed at the Carnegie Museum of Natural History (CM), the Denver Museum of Natural History (DMNH), and the Univer-

sity of California Museum of Paleontology (UCMP), and are catalogued with CM, DMNH, and UCMP numbers. DMNH numbers also refer to specimens that were catalogued in lots from specific locations in the cave. Thus the same catalogue number may appear repeatedly for multiple specimens from the same or different avian taxa. All specimens were measured with digital calipers, and values were rounded to the nearest 0.1 mm. Unless otherwise cited, all information on distribution and habitat of avian species in this chapter is taken from Bailey and Neidrach (1965) and Andrews and Righter (1992).

The ages of the deposits in Porcupine Cave are approximate because their determination relies almost entirely on biostratigraphic correlations based on arvicoline and sciurid rodents supplemented by magnetostratigraphic data; some of the latter data are equivocal. The best estimates place remains from the DMNH Velvet Room gray zone and below (horizons D–F at DMNH 644) in the middle Pleistocene (late to middle Irvingtonian, near and older than 780 Ka. Horizons A–C in the DMNH Velvet Room are placed at less than 780 Ka. Specimens from Mark's Sink (DMNH 1349, Velvet Room) probably are in part much older, possibly early Pleistocene (early Irvingtonian or latest Blancan, 1.3–1.6 Ma), as indicated by some of the arvicoline rodents. However, this is a mixed deposit with bones of different ages represented. Specimens from the Pit, levels 1–3, may equate with DMNH Velvet Room horizons D–F in age, and are estimated to lie somewhere in age between 600 and 800 Ka. Those from Pit levels 4–12 are at least in part older than 780 Ka, and probably are in the range of 800 Ka to possibly as old as 1.0 Ma. Deposits in the Badger Room (DMNH 942) probably correlate with levels 4–8 in the Pit. The Ferret Room (DMNH 1342) and Fissure Fill A (DMNH 1344) are also considered to be early middle Pleistocene in age, but they may be somewhat older than levels 8–12 in the Pit. (Chapter 20 reports a potential Blancan horse from Fissure Fill A, and chapter 19 recognizes two biostratigraphically old arvicolines in the Ferret Room.) A few specimens from Generator Dome

TABLE 12.1

Avian Taxa Identified from Early and Middle Pleistocene Deposits from Porcupine Cave

<i>Taxon</i>	<i>Number of Bones</i>	<i>MNI</i>
Early Pleistocene (earlier Irvingtonian and perhaps including Blancan)		
Pied-billed Grebe (<i>Podilymbus podiceps</i>)	2	1
Grebe (cf. <i>Podiceps</i> sp.)	1	1
Green-winged or Blue-winged Teal (<i>Anas crecca</i> or <i>A. discors</i>)	1	1
Anatidae, indeterminate	4	—
Hawk (<i>Buteo</i> sp.)	4	1
Accipitridae, indeterminate	1	—
Golden Eagle (cf. <i>Aquila chrysaetos</i>)	1	1
American Kestrel (<i>Falco sparverius</i>)	1	1
Falcon (<i>Falco</i> sp.)	1	1
Greater-sage Grouse (<i>Centrocercus urophasianus</i>) ^a	14	2
Spruce Grouse (<i>Falcipennis canadensis</i>) ^a	1	1
Blue Grouse (<i>Dendragapus</i> cf. <i>D. obscurus</i>) ^a	5	2
Phasianidae, indeterminate	2	—
Sora (cf. <i>Porzana carolina</i>)	1	1
Far Eastern or Eurasian Curlew (<i>Numenius madagascariensis</i> or <i>N. arquata</i>) ^a	1	1
Red-necked Phalarope (<i>Phalaropus</i> cf. <i>P. lobatus</i>) ^a	1	1
Scolopacidae, indeterminate	1	1
Gull (<i>Larus</i> sp.)	1	1
Great Horned Owl (<i>Bubo virginianus</i>)	1	1
Snowy Owl (<i>Nyctea scandiaca</i>) ^a	2	1
Long-eared or Short-eared Owl (<i>Asio</i> sp.)	1	1
Strigidae, indeterminate	1	1
Hairy Woodpecker (<i>Picoides villosus</i>)	1	1
Northern Flicker (<i>Colaptes auratus</i>)	7	2
American Crow (<i>Corvus brachyrhynchos</i>)	2	1
Common Raven (<i>Corvus corax</i>) ^a	2	1
Hirundinidae, indeterminate	1	1
Lark Sparrow (<i>Chondestes grammacus</i>) ^a	1	1
Lincoln's Sparrow (<i>Melospiza</i> cf. <i>M. lincolni</i>)	2	2
White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)	2	2
Sparrow (<i>Zonotrichia</i> sp.)	1	1
Dark-eyed Junco (<i>Junco hyemalis</i>) ^a	1	1
Lapland Longspur (<i>Calcarius lapponicus</i>)	3	3
Lapland Longspur (<i>Calcarius</i> cf. <i>C. lapponicus</i>)	1	1
Chestnut-collared Longspur (<i>Calcarius ornatus</i>)	2	2
Emberizidae, indeterminate	3	—
Gray-crowned Rosy-finch (<i>Leucosticte tephrocotis</i>) ^a	20	13
Black Rosy-finch (<i>Leucosticte atrata</i>) ^a	3	3
Rosy-finch (<i>Leucosticte</i> sp.)	1	1
Cassin's Finch (<i>Carpodacus cassinii</i>) ^a	1	1
Early middle Pleistocene (~1.0–0.78 Ma)		
Duck (<i>Anas</i> sp.)	1	1
Hawk (<i>Buteo</i> sp.)	1	1
Accipitridae, indeterminate	1	—
Virginia Rail (<i>Rallus</i> cf. <i>R. limicola</i>)	1	1
Black-billed Magpie (<i>Pica hudsonia</i>) ^a	1	1
Common Raven (<i>Corvus corax</i>)	2	1

TABLE 12.1 (continued)

<i>Taxon</i>	<i>Number of Bones</i>	<i>MNI</i>
Chipping Sparrow (<i>Spizella</i> cf. <i>S. passerina</i>) ^a	1	1
Song Sparrow (<i>Melospiza melodia</i>)	1	1
Emberizidae	1	1
Middle Pleistocene (stratigraphically younger than “early middle Pleistocene”)		
Goose (cf. <i>Anser</i> sp. or <i>Chen</i> sp.)	1	1
Duck (<i>Anas</i> sp.)	1	1
Anatidae, indeterminate	2	—
Hawk (<i>Buteo</i> sp.)	1	1
Golden Eagle (cf. <i>Aquila chrysaetos</i>)	1	1
Accipitridae, indeterminate	1	—
Greater-sage Grouse (<i>Centrocercus urophasianus</i>)	1	1
White-tailed Ptarmigan (<i>Lagopus</i> cf. <i>L. leucurus</i>)	1	1
Black-billed Magpie (<i>Pica hudsonia</i>)	1	1
American Crow (<i>Corvus brachyrhynchos</i>)	2	1
White-breasted Nuthatch (<i>Sitta carolinensis</i>) ^a	1	1
Nuthatch (<i>Sitta</i> sp.)	1	1
White-crowned Sparrow (<i>Zonotrichia leucophrys</i>) ^a	1	1
Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	1	1
Gray-crowned Rosy-finch (<i>Leucosticte tephrocotis</i>)	1	1
Late middle Pleistocene (? < 0.78 Ma)		
Duck (<i>Anas</i> sp.)	4	1
Redhead (<i>Aythya</i> cf. <i>A. americana</i>)	1	1
Anatidae, indeterminate	1	—
Hawk (<i>Buteo</i> sp.)	2	1
Accipitridae, indeterminate	1	—
Falcon (<i>Falco</i> sp.)	3	1
Greater-sage Grouse (<i>Centrocercus urophasianus</i>)	1	1
Pinyon Jay (<i>Gymnorhinus cyanocephalus</i>)	1	1
Horned Lark (<i>Eremophila alpestris</i>) ^a	4	3
Tree Swallow (<i>Tachycineta</i> cf. <i>T. bicolor</i>) ^a	1	1
Dark-eyed Junco (<i>Junco hyemalis</i>)	1	1
Brewer's Sparrow (<i>Spizella breweri</i>) ^a	1	1
Longspur (<i>Calcarius</i> sp.)	1	1
Gray-crowned Rosy-finch (<i>Leucosticte tephrocotis</i>)	2	2
Black Rosy-finch (<i>Leucosticte atrata</i>)	1	1
Total	154	95

^aEarliest fossil records known from North America.

(DMNH 1347), Will's Hole (DMNH 1350), and the Crystal Room (DMNH 1345) cannot be dated reliably. However, the Generator Dome deposit is possibly at least as old as or older than the lower Pit levels 8–12 and is so treated here (but see chapter 2 for caveats). Age control for Will's Hole is poor, but in this chapter it is regarded as about the same age as horizons C–F of the DMNH Velvet Room.

Table 12.1 lists all avian taxa identified from these localities sorted into approximate relative-age bins: early Pleistocene

(Mark's Sink); early middle Pleistocene (Pit levels 8–12, Badger Room, Fissure Fill A, Ferret Room, DMNH Velvet Room horizons G–I); middle Pleistocene (Pit levels 1–3, DMNH Velvet Room horizons C–F, Will's Hole); and late middle Pleistocene (DMNH Velvet Room horizons A–C). Specimens from mixed layers or provenances of unknown age (e.g., Crystal Room, Last Chance Pit) are not included in this table. Tables 10.1–10.13 list all avian taxa by locality. In the following section, the original excavation information in terms of numeric grid

and level designations is provided for the DMNH Velvet Room specimens, with the correlated horizon information, when known, in parentheses. (See chapter 2 for information about how the grid level designations translate into horizon designations; only the horizon designations have stratigraphic meaning.)

Systematic Paleontology

Class Aves

Order Podicipediformes

Family Podicipedidae

PODILYMBUS PODICEPS (LINNAEUS, 1758)

REFERRED MATERIAL Left humerus missing proximal end, DMNH 41118; left carpometacarpus, DMNH 41206.

PROVENANCE Location 1349, Mark's Sink.

DESCRIPTION These specimens are identical to the living *P. podiceps* in size and characters. This species is one of the longest-lived of any extant bird with a fossil record, possibly extending to the early Pliocene (5.2–4.5 Ma; Becker, 1987; Emslie, 1998).

CF. PODICEPS SP.

REFERRED MATERIAL Distal right humerus, DMNH 41240.

PROVENANCE Location 1349, Mark's Sink, level 27.

DESCRIPTION This specimen is similar in size and most characters to the living *Podiceps auritus* (Horned Grebe) but differs in having a relatively shallower impression of brachialis anticus and deep fossa on the entepicondylar prominence. It may represent an extinct species. However, of the five known fossil species that have been described from North America, all are either larger and more robust than *P. auritus* or are not represented by the humerus (see Murray [1967] and Emslie [1995] for a review of these fossil species). It is unlikely that DMNH 41240 represents any of these species. One extinct genus and species, *Pliolymbus baryosteus* Murray, 1967, is smaller than *P. auritus* and has a deep impression of brachialis anticus (Murray, 1967). Additional material is needed to assess further the taxonomic position of this fossil specimen.

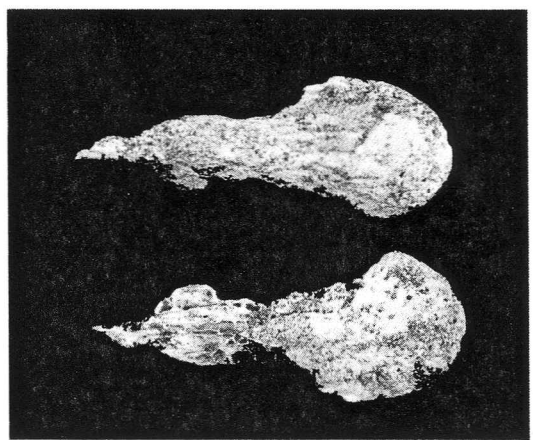
Order Anseriformes

Family Anatidae

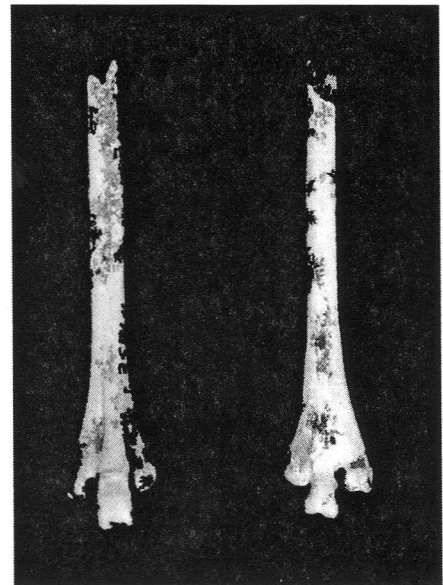
CF. ANSER SP. OR CHEN SP.

REFERRED MATERIAL Partial premaxilla, DMNH 12807 (fig. 12.1A).

PROVENANCE Location 644, Velvet Room, grid 16, level 19 (I).



A



B

FIGURE 12.1 (A) Premaxilla (DMNH 12807) of an unidentifiable goose, cf. *Anser* or *Chen* sp., in dorsal (top) and ventral (bottom) views. (B) Right tarsometatarsus (DMNH 35864) of *Numenius madagascariensis* or *N. arquata* (Far Eastern or Eurasian Curlew) in anterior (left) and posterior (right) views. Scale 1×, bar = 1 cm.

DESCRIPTION The relatively more posterior position of the nares on the premaxilla is one character that distinguishes *Anser* and *Chen* from *Branta*, which has nares placed farther anteriorly and nearer to the tip of the bill. The fossil is relatively larger than *A. albifrons*, *C. caerulescens*, and *C. rossii* and is too fragmentary for more specific identification. It may represent an undescribed species, but additional material is needed.

ANAS CRECCA LINNAEUS, 1758,
OR A. DISCORS LINNAEUS, 1766

REFERRED MATERIAL Left tarsometatarsus, DMNH 30205.

PROVENANCE Location 1349, Mark's Sink (PC-10).

DESCRIPTION This specimen compares well in size to either of these two species, but no osteological characters of this element reliably distinguish either taxon.

ANAS SP.

REFERRED MATERIAL Humeral right and left coracoids, DMNH 30198; right coracoid missing sternal end, DMNH 12037; proximal right and left scapulae, DMNH 30198; right carpometacarpus, DMNH 30196.

PROVENANCE 30196: Location 1342, Ferret Room (PC-3); 30198: Location 644, Velvet Room, grid 21, level 2 (B); 12037: Location 644, Velvet Room, grid 7, below level 23 (no age correlation).

DESCRIPTION All specimens except DMNH 12037 are similar in size to *Anas clypeata*. DMNH 12037 is from a small duck and probably represents a species of teal.

AYTHYA cf. A. AMERICANA (EYTON, 1838)

REFERRED MATERIAL Humeral right coracoid, DMNH 30191.

PROVENANCE Location 644, Velvet Room, grid 26, level 1 (A).

ANATIDAE, INDETERMINATE

REFERRED MATERIAL Partial furculum, DMNH 12351; two right coracoids with ends damaged, DMNH 30205; partial right coracoid, DMNH 10895; sternal half of right coracoid, DMNH 43331; left coracoid missing ends, DMNH 30161; distal right humerus, DMNH 30078; distal right carpometacarpus, CM 75128.

PROVENANCE 10895: Location 644, Velvet Room, grid 7, level 23 (no age correlation); 12351: Location 644, Velvet Room, grid 17, level 3 (B); 30161: Location 644, Velvet Room, mixed; 30078, 30205: Location 1349, Mark's Sink (PC-10); DMNH 43331: Location 1349, Mark's Sink, level 11; CM 75128: Badger Room.

DESCRIPTION These specimens are too fragmentary for specific identification. The furculum (DMNH 12351) is most similar to *Oxyura jamaicensis*, while the other specimens represent either *Anas*, *Aythya*, or *Bucephala*.

Order Accipitriformes

Family Accipitridae

BUTEO SP.

REFERRED MATERIAL Tip of premaxilla, DMNH 30155; right distal tarsometatarsus, DMNH 35391; two pedal phalanges, DMNH 30188 and 35819; four ungual phalanges, DMNH 13799, 35810, 35815, and 35816.

PROVENANCE 30155: Location 644, Velvet Room, grid 4, level 3 (A/B mixed); 30188: Location 644, Velvet Room, grid 21, level 2 (B); 13799: Location 942, Badger Room, mixed level; 35810, 35815, 35816, 35819: Location 1349, Velvet Room, Mark's Sink; 35391: Will's Hole.

DESCRIPTION These specimens represent hawks near the size of *Buteo jamaicensis* or *B. regalis* and are too fragmentary, or lack diagnostic features, for species identification.

CF. AQUILA CHRYSAETOS (LINNAEUS, 1758)

REFERRED MATERIAL Distal left femur, DMNH 30165; distal right tarsometatarsus, CM 65325; pedal phalanx, DMNH 30183.

PROVENANCE 30165: Location 644, Velvet Room, grid 11, 60 in. below marker (no age correlation); 30183: Location 644, Velvet Room, grid 20, level 3 (C); 65325: CM 1925, Pit, grid 1, level 1.

DESCRIPTION These specimens compare well to *Aquila chrysaetos* in characters, but DMNH 30165 (distal breadth, 24.6 mm; breadth distal shaft, 13.0 mm) and CM 65325 (distal breadth, 19.6 mm; middle trochlea breadth and depth, 6.2 and 9.1 mm) are slightly smaller in size than those of the living species ($N = 3$ males, USNM) and distinctly larger than those of females of *Buteo jamaicensis* and *B. regalis*. In *Haliaeetus leucocephalus*, the distal femur is relatively narrower and deeper when viewed distally, and the external trochlea of the tarsometatarsus is relatively higher than in *A. chrysaetos* and the fossil specimens.

ACCIPITRIDAE, INDETERMINATE

REFERRED MATERIAL Distal right humerus, DMNH 30202; pedal phalanx with ends gnawed, DMNH 30205; ungual phalanx, DMNH 13798; ungual phalanx missing proximal end, DMNH 16094.

PROVENANCE 16094: Location 644, Velvet Room, grid 4, level 4 (A/B mixed); 13798: Location 644, Velvet Room, grid 16, level 7 (E); 30205: Location 1349, Velvet Room, Mark's Sink; 30202: Location 1347, Generator Dome (PC-8).

DESCRIPTION These specimens are similar in size to an eagle but are too fragmentary for identification.

Family Falconidae

FALCO SPARVERIUS LINNAEUS, 1758

REFERRED MATERIAL Distal half of right tibiotarsus, DMNH 35742.

PROVENANCE Location 1349, Velvet Room, Mark's Sink.

FALCO SP.

REFERRED MATERIAL Left ulna missing ends, DMNH 30189; proximal left femur, DMNH 35721; distal left tarsometatarsus, DMNH 9801; two ungual phalanges, DMNH 9924.

PROVENANCE 9801: Location 644, Velvet Room, grid 3, level 7 (mixed); 9924: Location 644, Velvet Room, grid 5, level 5 (B); 30189: Location 644, Velvet Room grid 25, level 2 (B); 35721: Location 1349, Velvet Room, Mark's Sink.

DESCRIPTION The ulna, femur, and tarsometatarsus are within the size range of *Falco peregrinus* or *F. mexicanus*, but they are too fragmentary for positive identification. The phalanges (DMNH 9924) are from a large falcon, near the size of *F. rusticolus*.

Order GALLIFORMES

Family PHASIANIDAE

CENTROCERCUS UROPHASIANUS (BONAPARTE, 1827)

REFERRED MATERIAL Two premaxilla, DMNH 30204 and CM 73359; three distal mandibular symphyses, DMNH 8830, 8924, and 35383; two humeral ends of right coracoid, DMNH 30205 and 35743; humeral end of left coracoid, DMNH 30079; proximal right scapula, DMNH 30205; fragment of furculum, DMNH 30205; distal left humerus, DMNH 35385; two right carpometacarpi missing ends, DMNH 30205; two distal left tibiotarsi, DMNH 9849 and 30205; right and left tarsometatarsi with damaged proximal ends, DMNH 30205; right tarsometatarsus, DMNH 35817; right tarsometatarsus missing ends, DMNH 30205.

PROVENANCE 8830: Location 644, Velvet Room, grid 1, level 7 (mixed); 9849: Location 644, Velvet Room, grid 5, level 8 (C); 8924: Location 644, Velvet Room, grid 7, level 2 (A); 35385: Location 644, Velvet Room (no age correlation); 30204: Location 644, Mark's Sink; 30079, 30205, 35383, 35743, and 35817: Location 1349, Velvet Room, Mark's Sink; CM 73359: CM Velvet Room 1932, undifferentiated grid and level.

MEASUREMENTS See table 12.2.

DESCRIPTION These specimens compare well in size and characters to this species. The premaxilla (DMNH 30204) is slightly shorter than in modern specimens (approximately 14% shorter bill length and 7% smaller depth than the average for $N=8$ females; table 12.2). The recently recognized *Centrocercus minimus* (Gunnison Sage-Grouse) (Young et al., 2000) has a culmen length 27% smaller than in *C. urophasianus*

(Hupp and Braun, 1991), but no specimens of the former were available for comparison. Since *C. minimus* is distinguished by its smaller size, voice, and behavior (Young et al., 1994, 2000), acquisition and measurement of skeletal material from this population is warranted. *C. urophasianus* is resident in mountain parks and other areas where sagebrush is present. The fossils reported here represent the earliest record of this species in North America. It also has been reported from the late Pleistocene of Oregon, Nevada, and New Mexico (Brodkorb, 1964).

FALCIPENNIS CANADENSIS (LINNAEUS, 1758)

REFERRED MATERIAL Distal mandibular symphysis, DMNH 6706; manubrium of sternum, DMNH 8830; proximal left humerus, DMNH 6706; distal right humerus, DMNH 8830; proximal right carpometacarpus, DMNH 30077.

PROVENANCE 6706: Location 644, Velvet Room, grid 1, level 4 (mixed); 8830: Location 644, Velvet Room, grid 1, level 7 (mixed); 30077: Location 1349, Velvet Room, Mark's Sink.

DESCRIPTION These specimens are distinguished as *Falcipennis canadensis* from *Dendragapus obscurus* primarily by the relatively smaller size of the former. The manubrium of the sternum also is distinct in these species. DMNH 8830 has a relatively longer and narrower ventral manubrial spine, with a smaller foramen passing through the base of this spine, as found in *F. canadensis*, rather than exhibiting the condition found in *D. obscurus* (manubrium shorter and broader with a larger foramen). These specimens represent the first fossil record of this species in Colorado and the earliest known in North America. *F. canadensis* occurs in coniferous forests in Canada, Alaska, and south to Montana with one record of a bird shot near Palmer Lake, Colorado, in 1896 (Bailey and Niedrach, 1965). The fossils reported here indicate that this species occurred more commonly in the southern Rocky Mountains during the Pleistocene.

LAGOPUS CF. L. LEUCURUS (RICHARDSON, 1831)

REFERRED MATERIAL Right coracoid, DMNH 30206.

PROVENANCE Location 1350, Will's Hole (PC-11).

DESCRIPTION This specimen is recognized as *Lagopus*, and not *Bonasa*, by the morphology and relative size of the glenoid facet and head, which are more robust in the latter. It most closely resembles *Lagopus leucurus* in size; *L. mutus* and *L. lagopus* are larger and more robust in the shaft of the coracoid. *L. leucurus* is resident in alpine areas of Colorado today.

DENDRAGAPUS CF. D. OBSCURUS (SAY, 1823)

REFERRED MATERIAL Humeral left coracoid, DMNH 8530; two distal left humeri, DMNH 35759 and 35818; two distal right humeri, DMNH 35740 and 35809; right carpometacarpus, CM 73360; left carpometacarpus missing proximal end, DMNH 8530.

TABLE 12.2
Measurements of Premaxillae of *Centrocercus urophasianus*
Compared to the Fossil Specimen from Porcupine Cave

Specimens	Length	Breadth	Depth	Breadth of Nasal Bar
Males (N = 8)	12.8 ± 0.49 (11.9–13.4)	10.9 ± 0.31 (10.6–11.5)	8.23 ± 0.29 (7.8–8.6)	3.14 ± 0.29 (2.9–3.6)
Females (N = 8)	11.1 ± 0.71 (10.0–12.4)	9.1 ± 0.64 (8.2–9.8)	7.1 ± 0.52 (5.9–7.6)	2.5 ± 0.32 (1.8–2.7)
Fossil: DMNH 30204	9.5	9.8	6.6	2.3

NOTE: Measurements are in millimeters. Measurements are mean ± SD with range in parentheses.

PROVENANCE 8530: Location 644, Velvet Room, grid 1, level 10 (mixed); 35740, 35759, 35809, and 35818: Location 1349, Velvet Room, Mark's Sink; CM 73360: CM 1932, undifferentiated.

DESCRIPTION These specimens compare closely in size and characters to this species. CM 73360 measures length, 35.4 mm; proximal breadth and depth, 5.3 and 10.1 mm; least breadth and depth of shaft, 3.8 and 3.2 mm; and distal breadth and depth, 5.5 and 7.3 mm. It is similar in size to two female specimens of *Dendragapus obscurus* at USNM.

PHASIANIDAE, INDETERMINATE

REFERRED MATERIAL Distal mandibular symphysis, DMNH 41138; two right tarsometatarsi missing ends, DMNH 8849 and 41128.

PROVENANCE 8849: Location 644, Velvet Room, grid 1, level 2 (mixed); 41128: Location 1349, Mark's Sink, level 9; 41138: Location 1349, Mark's Sink, level 13.

Order Gruiformes

Family Rallidae

RALLUS CF. R. LIMICOLA

REFERRED MATERIAL Proximal right humerus, DMNH 30202.

PROVENANCE Location 1347, Generator Dome (PC-8).

DESCRIPTION This specimen compares well in characters to specimens of *Rallus limicola* from Florida examined at FLMNH but is slightly more robust in size. No specimens of this rail from more northern regions of North America were available for comparison. *R. limicola* is a common resident in Colorado in wet meadows and marshes in mountain parks and other regions.

CF. PORZANA CAROLINA (LINNAEUS, 1758)

REFERRED MATERIAL Right tarsometatarsus missing proximal end, DMNH 30205.

PROVENANCE Location 1349, Mark's Sink (PC-10).

DESCRIPTION The specimen also compares closely to *Rallus limicola* in size and features; however, the posterior proximal border of the middle trochlea is more pointed in *Porzana* and DMNH 30205 and more rounded and blunt in *Rallus*.

Order Charadriiformes

Family Scolopacidae

NUMENIUS MADAGASCARIENSIS (LINNAEUS, 1766)

OR N. ARQUATA (LINNAEUS, 1758)

REFERRED MATERIAL Distal half of right tarsometatarsus, DMNH 35864 (fig. 12.1B).

PROVENANCE Location 1349, Velvet Room, Mark's Sink, level 19.

MEASUREMENTS See table 12.3.

DESCRIPTION DMNH 35864 is much larger and more robust than tarsometatarsi of male *Numenius americanus*, *N. borealis*, *N. minutus*, *N. tahitiensis*, and *N. phaeopus*; it is most similar in size and characters to *N. madagascariensis* and *N. arquata*. These species are both large curlews whose tarsometatarsi overlap in most measurements (table 12.3), and they cannot be distinguished by osteological characters. *N. madagascariensis* has been reported in North America from the Aleutian and Pribilof islands as a regular spring migrant and in British Columbia (accidental); it is found primarily in Siberia, Mongolia, and southeast Asia. *N. arquata* has occurred as accidental records in Newfoundland, New York, and Massachusetts (American Ornithologists' Union, 1998). The specimen reported here is the first fossil record of a large curlew representing a European or Asian species in North America.

DISCUSSION The identification of *N. madagascariensis* or *N. arquata* from the early Pleistocene of Colorado adds to a growing list of avian taxa with current European and Asiatic distributions that occurred in the late Pliocene or early Pleistocene of continental North America. Other taxa in this category include shelducks (Anatidae, Tribe Tadornini)

TABLE 12.3

Measurements of Tarsometatarsi of *Numenius* Species Compared to the Fossil Specimen from Porcupine Cave

Species	LBS	LDS	DB	MTB	MTD
<i>Numenius arquata</i> (N = 13; 6 M, 7 F)	3.9 ± 0.15 (3.7–4.1)	3.0 ± 0.18 (2.7–3.3)	10.3 ± 0.6 (9.2–11.6)	3.9 ± 0.23 (3.6–4.3)	4.7 ± 0.20 (4.4–5.1)
<i>Numenius americanus</i> (N = 7; 6 M, 1 F)	3.6 ± 0.28 (3.3–4.1)	2.5 ± 0.21 (2.3–2.7)	9.1 ± 0.54 (8.4–9.9)	3.5 ± 0.16 (3.4–3.7)	4.2 ± 0.24 (3.8–4.4)
<i>Numenius madagascariensis</i> (N = 2)					
USNM 500255 (M)	3.8	3.4	11.0	4.1	4.9
USNM 500254 (F)	4.1	3.3	11.1	4.1	4.7
Fossil: DMNH 35864	4.3	3.2	10.8	4.1	4.8

NOTES: Measurements are in millimeters. LBS, least breadth of shaft; LDS, least depth of shaft; DB, distal breadth; MTB, middle tarsus breadth; MTD, middle tarsus depth. Measurements for *N. arquata* and *N. americanus* are mean ± SD with range in parentheses.

represented by the extinct genera *Anabernicula* and *Brantadorna* from Florida and the western United States, pygmy geese (Anatidae, Tribe Anatini) represented by the extinct species *Helonetta brodkorbi* from Florida, and storks (Ciconiidae, *Ciconia*) represented by *C. maltha* from Florida and the western United States (Emslie, 1992, 1998). In addition, fossil birds from the early Pliocene of North Carolina include *Larus* aff. *L. minutus* (Little Gull), *Grus* aff. *G. antigone* (Sarus Crane), *Haematopus* aff. *H. ostralegus* (Common Oystercatcher), *Tringa* magn. *T. ochropus* (Green Sandpiper), and *Ardea* aff. *A. cinerea* (Gray Heron) (Olson and Rasmussen, 2001). Notably, all these taxa are affiliated with wetland environments, and it is possible that wetland species, owing to climatic conditions in the past, were able to extend their distributional ranges more easily during the ice ages than other avian taxa. *N. madagascariensis* currently nests in dry grasslands, near wetlands and sphagnum bogs where it prefers to forage, in Siberia and China and migrates to Australia in winter (Johnsgard, 1981; Ueta and Antonov, 2000). *N. arquata* breeds in similar habitat from northwestern Europe to central Asia (Johnsgard, 1981).

PHALAROPUS CF. *P. LOBATUS* (LINNAEUS, 1758)

REFERRED MATERIAL Right carpometacarpus, DMNH 35728.

PROVENANCE Location 1349, Velvet Room, Mark's Sink.

DESCRIPTION This specimen measures length, 18.5 mm; proximal breadth and depth, 2.2 and 4.8 mm; distal breadth and depth, 2.3 and 2.7 mm. This specimen was also compared to *Phalaropus tricolor* and *P. fulicaria*, both of which are relatively larger than *P. lobatus*. It is tentatively referred to this last species based on its small size and characters. *P. lobatus* is a common migrant in eastern Colorado and uncommon to rare in mountain parks and valleys, where it prefers wetlands, ponds, and streams.

CF. SCOLOPACIDAE, INDETERMINATE

REFERRED MATERIAL Distal half of right humerus (damaged), DMNH 35740.

PROVENANCE Location 1349, Velvet Room, Mark's Sink.

DESCRIPTION This specimen is too fragmentary for generic identification, but it appears to represent a shorebird similar to a small *Numenius*.

Family Laridae

LARUS SP.

REFERRED MATERIAL Distal half of right tarsometatarsus missing external trochlea, DMNH 35758.

PROVENANCE Location 1349, Velvet Room, Mark's Sink, level 19.

DESCRIPTION This specimen is from a small gull, near the size of *Larus pipixcan*, but is too fragmentary for specific identification.

Order Strigiformes

Family Strigidae

BUBO VIRGINIANUS (GMELIN, 1788)

REFERRED MATERIAL Pedal phalange, DMNH 35819.

PROVENANCE Location 1349, Velvet Room, Mark's Sink.

NYCTEA SCANDIACA (LINNAEUS, 1758)

REFERRED MATERIAL Distal mandibular symphysis, DMNH 30153; three pedal phalanges, DMNH 30205 (2) and 30153.

PROVENANCE 30153: Location 644, Velvet Room, grid 2, level 3 (mixed); 30205: Location 1349, Velvet Room, Mark's Sink (PC-10).

DESCRIPTION The mandibular symphyses of *Nyctea scandiaca* and DMNH 30153 are relatively broader and larger than those in *Bubo* or *Strix*. The pedal phalanges are relatively shorter and more robust in *Nyctea* and the fossil specimens than in *Bubo virginianus* and are larger than in *Strix nebulosa*. *N. scandiaca* occurs primarily in Arctic tundra in Canada and Alaska, but it ranges southward sporadically and has been recorded in the northeastern plains and mountain parks of Colorado. The fossils reported here represent the earliest fossil record for the species. It has also been reported from the late Pleistocene of Wyoming (Emslie, 1985).

ASIO OTUS (LINNAEUS, 1758)

REFERRED MATERIAL Right femur with proximal end damaged, DMNH 30178.

PROVENANCE Location 644, Velvet Room, bilge level (mixed).

DESCRIPTION The specimen measures length, circa 51.5 mm; distal breadth, 9.1 mm. *Asio flammeus* is similar to *A. otus* but is slightly larger in size (Emslie, 1982). The measurements of DMNH 30178 more closely match those of *A. otus*. *A. otus* occurs in valleys and mountain parks throughout Colorado, including mixed coniferous forests near marshes or wet meadows.

ASIO SP.

REFERRED MATERIAL Humeral end of left coracoid, DMNH 43341.

PROVENANCE Location 1349, Velvet Room, Mark's Sink.

DESCRIPTION This specimen is too fragmentary for specific identification but is similar in size and characters to either *Asio flammeus* or *A. otus*.

STRIGIDAE, INDETERMINATE

REFERRED MATERIAL Distal mandibular symphysis, DMNH 35730.

PROVENANCE Location 1349, Velvet Room, Mark's Sink.

DESCRIPTION This specimen is most similar in size and characters to *Surnia ulula*, but it differs in position and size of foramina on the external surfaces. It is too fragmentary for more positive identification.

Order Piciformes

Family Picidae

PICOIDES VILLOSUS (LINNAEUS, 1766)

REFERRED MATERIAL Distal mandibular symphysis, DMNH 30080.

PROVENANCE Location 1349, Velvet Room, Mark's Sink.

DESCRIPTION This specimen is referred to *Picoides*, and not *Colaptes*, by its relatively longer symphysis (short in *Colaptes*). In addition, *Melanerpes* has a shallower symphysis than *Picoides*; in *Sphyrapicus*, the proximal opening to a middle canal in the symphysis is more open and excavated than in *Picoides*. The fossil is recognized as *P. villosus* by its similarity in symphyseal length and breadth (much broader in *P. tridactylus*, broader and longer in *P. arcticus*, smaller in *P. pubescens*).

COLAPTES AURATUS (LINNAEUS, 1758)

REFERRED MATERIAL Distal right humerus, DMNH 30205; left ulna, DMNH 30205; distal left ulna, DMNH 30077; proximal left carpometacarpus, DMNH 30205; distal left carpometacarpus, DMNH 43321; two distal right tarsometatarsi, DMNH 30203 and 41145.

PROVENANCE 30077, 30203, and 30205: Location 1349, Mark's Sink (PC-10); 41145: Location 1349, Mark's Sink, level 16; 43321: Location 1349, Mark's Sink.

Order Passeriformes

Family Corvidae

GYMNORHINUS CYANOCEPHALUS

REFERRED MATERIAL Proximal half of left mandible, DMNH 35392.

PROVENANCE Location 644, Velvet Room, grid 11, level 4 (B).

DESCRIPTION This specimen compares well in size and characters to the living species. It was also compared to *Cyanocitta stelleri*, *Aphelocoma californica*, *Nucifraga columbiana*, and *Perisoreus canadensis*. All these genera are distinct, especially in their relative size and the morphology of the post-articular and articular processes of the mandible. DMNH 35392 most closely matches *Gymnorhinus cyanocephalus* in these features.

DISCUSSION This specimen represents the earliest fossil record of this species. It has also been reported from the late Pleistocene of Mexico and New Mexico and from archaeological sites in Utah and Arizona (Brodkorb, 1978; Steadman et al., 1994a). *G. cyanocephalus* is found primarily in pinyon-juniper forests in Colorado today, at an elevational range of 1680–2440 m.

PICA HUDSONIA (SABINE, 1823)

REFERRED MATERIAL Left humerus missing proximal end, DMNH 11332; left carpometacarpus, DMNH 30195.

PROVENANCE 11332: Location 644, Velvet Room, grid 9, level 6 (C); 30195: Location 1342, Ferret Room.

DESCRIPTION These specimens compare closely in size and characters to the living species. *Pica hudsonia* occurs in riparian zones and mountain parks throughout Colorado today.

CORVUS BRACHYRHYNCHOS BREHM, 1822

REFERRED MATERIAL Left coracoid missing ends, DMNH 30205; distal right tibiotarsus, DMNH 41100; distal right tarsometatarsus, DMNH 43342; distal left tarsometatarsus, CM 75132.

PROVENANCE 30205: Location 1349, Mark's Sink (PC-10); 43342: Location 1349, Mark's Sink, level 25; 41100: Location 644, Velvet Room, grid 7, level 16 (E); CM 75132: Badger Room.

DESCRIPTION The specimen is distinctly smaller than *Corvus corax* and compares well in size and characters to *C. brachyrhynchus*.

CORVUS CORAX LINNAEUS, 1758

REFERRED MATERIAL Right humerus missing distal end, UCMP 175013; proximal half of left carpometacarpus, CM 73316; humeral half of right coracoid, DMNH 30197; proximal right femur, DMNH 30205; left tibiotarsus missing proximal end, CM 73315; right tarsometatarsus missing portion of proximal end, DMNH 30198; distal right tarsometatarsus, DMNH 10974.

PROVENANCE CM 73315, 73316: Location CM 2203, Crystal Room (no age correlation); 30197 and 30198: Location 942, Badger Room (PC-1); 30205: Location 1349, Mark's Sink (PC-10); 10974: Location 644, Velvet Room, grid 7, level 22 (no age correlation); 175013: Location 1349, Mark's Sink, grid 1, level 1, 2, or 3.

DESCRIPTION These specimens are slightly smaller and more slender than modern specimens of *Corvus corax* but are distinctly larger than *C. cryptoleucus*. They probably represent a slightly smaller temporal form of the living species. Magish and Harris (1976) described an extinct raven, *C. neomexicanus*, from the late Pleistocene of New Mexico. Later, additional material was tentatively referred to this species from the late Pleistocene of Utah (Emslie and Heaton, 1987). This extinct raven is distinguished from *C. corax* only by its smaller size, and Brodkorb (1978) considered it to be synonymous with *C. corax*. The tarsometatarsus (DMNH 30198) has an approximate length of 64.1 mm and depth of the distal middle trochlea of 5.1 mm; DMNH 10974 is 5.5 mm in the latter measurement. These measurements more closely approximate *C. corax* in size, as documented by Magish and Harris (1976:table 1), although the trochlea depth of DMNH 30198 is small. Based on these comparisons, the Porcupine Cave material is not considered to represent the extinct species *C. neomexicanus*.

Family Alaudidae

EREMOPHILA ALPESTRIS (LINNAEUS, 1758)

REFERRED MATERIAL Three premaxillae, DMNH 30160, 30171, and 30179; distal mandibular symphysis, DMNH 30082.

PROVENANCE 30160: Location 644, Velvet Room, grid 7, level 5 (B); 30171: Location 644, Velvet Room, grid 15, level 2 (B); 30179: Location 644, Velvet Room, grid 20, level 2 (B); 30082: Location 644, Velvet Room, grid 12, level 5 (B).

Family Hirundinidae

TACHYICINETA CF. T. BICOLOR VIEILLOT, 1808

REFERRED MATERIAL Premaxilla, DMNH 30097.

PROVENANCE Location 644, Velvet Room, grid 9, level 2 (B).

DESCRIPTION The specimen differs from *Hirundo rustica* and *Riparia riparia*, which have a slightly longer and narrower bill, and from *H. pyrrhonota*, which has a nasal bar that rises more steeply posteriorly from the premaxilla than in *Tachycineta bicolor*. *T. bicolor* is a common summer resident throughout Colorado today.

HIRUNDINIDAE, INDETERMINATE

REFERRED MATERIAL Right humerus, DMNH 30203.

PROVENANCE Location 1349, Velvet Room, Mark's Sink (PC-10).

Family Sittidae

SITTA CAROLINENSIS LATHAM, 1790

REFERRED MATERIAL Distal mandibular symphysis, DMNH 30207.

PROVENANCE Location 1350, Will's Hole (PC-11).

DESCRIPTION This specimen compares well in size and characters to *Sitta carolinensis*; the mandibular symphyses of *S. canadensis* and *S. pygmaea* are smaller than that in *S. carolinensis*.

SITTA SP.

REFERRED MATERIAL Distal mandibular symphysis missing tip, DMNH 43317.

PROVENANCE Location 644, Velvet Room, grid 21, level 7A (C).

DESCRIPTION This specimen is similar to *Sitta carolinensis* and *S. canadensis* in size and characters but it cannot be reliably distinguished to either species.

Family Troglodytidae

CF. THRYOTHORUS SP.

REFERRED MATERIAL Distal mandibular symphysis, DMNH 8528.

PROVENANCE Location 644, Velvet Room, grid 1, level 10 (mixed).

DESCRIPTION This specimen is larger than those in *Salpinctes obsoletus*, *Troglodytes aedon*, *T. troglodytes*, *Thryomanes bewickii*, *Catherpes mexicanus*, *Cistothorus platensis*, and *C. palustris*, and distinctly smaller than that in *Campylorhynchus brunneicapillus*. It compares most closely in size and features to *Thryothorus ludovicianus*, but in lateral view the dentary in this species begins curving downward sooner than that in the fossil specimen. This specimen may represent an extinct species of wren, but additional material and further comparisons to living taxa are needed.

Family Emberizidae

SPIZELLA CF. S. PASSERINA (BECHSTEIN, 1798)

REFERRED MATERIAL Premaxilla, DMNH 30195.

PROVENANCE Location 1342, Ferret Room.

DESCRIPTION This specimen compares well in size and characters to this species; among other species in this genus, the premaxilla is slightly smaller and narrower (*Spizella breweri*, *S. pusilla*, and *S. pallida*) or larger and broader (*S. arborea*).

SPIZELLA BREWERI CASSIN, 1856

REFERRED MATERIAL Mandible missing proximal right end, DMNH 30164.

PROVENANCE Location 644, Velvet Room, grid 8/8A, level 2 (A).

DESCRIPTION This specimen is smaller and broader at the symphysis than those in *Spizella pallida* and *S. passerina*, smaller and narrower at the symphysis than those in *S. arborea*, *S. atrogularis*, and *S. pusilla*, and compares well in size and characters to *S. breweri*, including in the size and shape of the mandibular foramen. *S. breweri* is common in sagebrush and rabbitbrush habitats, but also occurs in pinyon-juniper forest throughout Colorado today (Rising, 1996).

CHONDESTES GRAMMACUS (SAY, 1823)

REFERRED MATERIAL Distal mandibular symphysis, DMNH 30081.

PROVENANCE Location 1349, Velvet Room, Mark's Sink.

DESCRIPTION *C. grammacus* is a common summer resident in valleys and foothills throughout Colorado today but

is uncommon in mountain parks. It prefers grasslands and shrublands for breeding.

MELOSPIZA MELODIA (WILSON, 1810)

REFERRED MATERIAL Distal mandibular symphysis, DMNH 35389.

PROVENANCE Location 1347, Generator Dome (PC-8).

DESCRIPTION *M. melodia* is a common breeding bird in mountain parks near rivers and wetlands, and in riparian zones, throughout Colorado.

MELOSPIZA CF. M. LINCOLNII (AUDUBON, 1834)

REFERRED MATERIAL Two premaxillae, DMNH 43307 and 43338.

PROVENANCE 43307: Location 1349, Velvet Room, Mark's Sink; 43338: Location 1349, Velvet Room, Mark's Sink, level 24.

DESCRIPTION These specimens compare best in size and features to this species. *Melospiza georgiana* has a longer and narrow beak, while *M. melodia* is longer and more robust. Specimens of *Zonotrichia leucophrys*, *Z. querula*, and *Z. albicollis* also are much larger and more robust than the fossil material.

ZONOTRICHIA LEUCOPHRYS (FORSTER, 1772)

REFERRED MATERIAL Right proximal mandible, DMNH 12765; two distal mandibular symphyses, DMNH 35753 and 41119.

PROVENANCE 12765: Location 644, Velvet Room, grid 8/8A, level 11 (E); 35753 and 41119: Location 1349, Mark's Sink.

DESCRIPTION These specimens compare well in size and characters to those in the living species except for a slightly higher ramus in DMNH 12765. *Zonotrichia leucophrys* occurs at all elevations in Colorado today, frequenting alpine tundra, riparian zones, and mountain parks for breeding, and wintering in the foothills and plains.

ZONOTRICHIA SP.

REFERRED MATERIAL Distal mandibular symphyses, DMNH 43343.

PROVENANCE Location 1349, Velvet Room, Mark's Sink.

DESCRIPTION This specimen is similar to *Zonotrichia leucophrys* but is too fragmentary for specific identification.

JUNCO HYEMALIS (LINNAEUS, 1758)

REFERRED MATERIAL Premaxilla, DMNH 30164; distal mandibular symphysis, DMNH 35754.

PROVENANCE 30164: Location 644, Velvet Room, grid 8/8A, level 2 (A); 35754: Location 1349, Velvet Room, Mark's Sink, level 19.

DESCRIPTION The ventral surface of the premaxilla in *Junco* and DMNH 30164 has more distinct concavities and a more distinct midline ridge compared to *Zonotrichia* and *Melospiza*. *J. hyemalis* occurs throughout Colorado today.

CALCARIUS LAPPONICUS (LINNAEUS, 1758)

REFERRED MATERIAL Three premaxillae, DMNH 35722, 41207, and 41220.

PROVENANCE 35722: Location 1349, Mark's Sink, level 16; 41207: Location 1349, Mark's Sink, level 19; 41220: Location 1349, Mark's Sink, level 22.

DESCRIPTION These specimens were also compared to *Calcarius ornatus*, *C. pictus*, and *C. mccownii*. In *C. lapponicus* and *C. pictus*, the premaxillae are slightly smaller and narrower at the base than in *C. ornatus*. *C. mccownii* is distinctly larger, with a longer and more robust bill, than *C. ornatus*, *C. lapponicus*, and *C. pictus*. Compared to *C. pictus*, *C. lapponicus* has a slightly longer and narrower bill. *C. lapponicus* occurs primarily in the eastern plains of Colorado during winter, but it also has been reported from mountain parks and valleys. It prefers grassland and prairie habitats.

CALCARIUS CF. C. LAPPONICUS

REFERRED MATERIAL Premaxilla, DMNH 35729.

PROVENANCE Location 1349, Velvet Room, Mark's Sink.

DESCRIPTION The specimen is too fragmentary for positive identification but most closely matches *Calcarius lapponicus* in size and characters.

CALCARIUS CF. C. PICTUS (SWAINSON, 1832)

REFERRED MATERIAL Premaxilla, DMNH 43452.

PROVENANCE Last Chance Pit, unit 2, level 7.

DESCRIPTION This specimen is larger and more robust than *Calcarius lapponicus*, narrower at the base than in *C. ornatus*, and smaller than *C. mccownii*. It most closely matches the characteristics of *C. pictus* and is tentatively referred to that species. *C. pictus* previously has not been reported from Colorado. It prefers dry, grassy environments and tundra and breeds in Alaska and Canada. It migrates primarily through the Great Plains to Kansas and Oklahoma in winter (American Ornithologists' Union, 1998).

CALCARIUS ORNATUS (TOWNSEND, 1837)

REFERRED MATERIAL Two premaxillae, DMNH 35760 and 43311.

PROVENANCE Location 1349, Velvet Room, Mark's Sink.

DESCRIPTION These specimens compare well in size and features to this species as described previously. *C. ornatus* is a common summer resident in the plains of eastern Colorado and a migrant in western valleys. It prefers short- and mixed-grass prairie habitats that are frequently disturbed by fires or grazing (Hill and Gould, 1997).

CALCARIUS SP.

REFERRED MATERIAL Proximal left mandible, DMNH 30160.

PROVENANCE Location 644, Velvet Room, grid 7, level 5 (B).

DESCRIPTION This specimen is most similar to *Calcarius lapponicus* in characters but is slightly smaller than those in three females (FLMNH); no male specimens were available.

EMBERIZIDAE, INDETERMINATE

REFERRED MATERIAL Four distal mandibular symphysis, DMNH 35724, 35736, 41106, and 41119.

PROVENANCE 35724, 35736, and 41119: Location 1349, Velvet Room, Mark's Sink; 41106: Location 1347, Generator Dome, level 1.

DESCRIPTION These specimens are too fragmentary for identification.

Family Icteridae

AGELAIUS PHOENICEUS (LINNAEUS, 1766)

REFERRED MATERIAL Distal mandibular symphysis, DMNH 8742.

PROVENANCE Location 644, Velvet Room, grid 7, level 6 (C).

Family Fringillidae

LEUCOSTICTE TEPHROCOTIS (SWAINSON, 1832)

REFERRED MATERIAL Ten premaxillae, DMNH 10552, 30081, 30097, 35747, 35749, 35801, 35806, 41119, 43313, and 43450; 14 distal mandibular symphyses, DMNH 30081 (2), 35383, 35397, 35746, 35812, 35813, 41119 (2), 41130, 41210, 43312, 43315, and 43327.

PROVENANCE 30097: Location 644, Velvet Room, grid 9, level 2 (B); 35397: Location 644, Velvet Room, grid 11, level 5 (C); 10552: Location 644, Velvet Room, grid 6, level 1 (A); 30081, 35383, 35746, 35747, 35749, 35801, 35806, 35812, 35813, 41119, 41130, 41210, 43312, 43313, 43315, and 43327: Location 1349, Velvet Room, Mark's Sink; 43450: Location 2433, Last Chance Pit.

DESCRIPTION This species is recognized by the premaxilla, which narrows toward the distal tip and is slightly broader and more robust in *Leucosticte tephrocotis* as opposed to a slightly more convex margin to the tip and narrower shape in *L. atrata*, and by a slightly shorter mandibular symphysis as compared to the latter species; no specimens of *L. australis* were available for comparison. *L. tephrocotis* is a winter resident in the foothills and mountain parks of Colorado, where it prefers meadows and shrublands.

LEUCOSTICTE ATRATA RIDGWAY, 1874

REFERRED MATERIAL Four distal mandibular symphyses, DMNH 30080 (2), 30081, and 30097.

PROVENANCE 30080 and 30081: Location 1349, Velvet Room, Mark's Sink; 30097: Location 644, Velvet Room, grid 9, level 2 (B).

DESCRIPTION The symphyses are slightly longer in these fossils and in *Leucosticte atrata* compared to a shorter symphysis in *L. tephrocotis*. *L. atrata* is an irregular to common winter resident in mountain parks and meadows of western Colorado.

LEUCOSTICTE SP.

REFERRED MATERIAL Distal mandibular symphysis, DMNH 43316.

PROVENANCE Location 1349, Velvet Room, Mark's Sink.

DESCRIPTION This specimen is too fragmentary for specific identification.

CARPODACUS CASSINII BAIRD, 1854

REFERRED MATERIAL Distal mandibular symphysis, DMNH 30080.

PROVENANCE Location 1349, Velvet Room, Mark's Sink.

DESCRIPTION The symphysis is longer and narrower in this species and the fossil specimen compared to shorter and broader symphyses in *Carpodacus purpureus* and *C. mexicanus*. *Carpodacus cassinii* is a common resident throughout the mountains of Colorado, where it breeds primarily in coniferous forests.

PASSERIFORMES, INDETERMINATE

REFERRED MATERIAL Two right coracoids, DMNH 30190 and 35811; three right coracoids, DMNH 30203; right coracoid missing sternal end, DMNH 35757; left coracoid, DMNH 35744; humeral half left coracoid, DMNH 30203; three left and one right humeri, DMNH 30203; three right humeri, DMNH 30202; four right humeri, DMNH 30190, 35745, 35804, and 35807; distal right humerus, DMNH 35752; distal right humerus, shaft of left humerus, DMNH 30202; two left

humeri, DMNH 35802 and 35814; distal left and proximal right humeri, DMNH 30203; two distal left humeri, DMNH 35740; distal half left humerus, DMNH 35751; two right ulnae, DMNH 30203; two right ulnae, DMNH 35761 and 35800; proximal half right ulna, DMNH 35755; proximal right and proximal left ulnae, DMNH 30203; distal half right ulna, DMNH 30203; proximal left and two distal right ulnae, distal left ulna, DMNH 35762; right carpometacarpus, DMNH 35803; two right and one left carpometacarpi, DMNH 30203; left carpometacarpus, DMNH 35808; left carpometacarpus missing ends, DMNH 30190; left femur, DMNH 30203; left tibiotarsus missing distal end, DMNH 30203; right tarsometatarsus, DMNH 30203.

PROVENANCE These specimens were recovered from various excavated areas of the cave.

Discussion

Prior to the discovery of Porcupine Cave, little information existed about early and middle Pleistocene avifauna from the intermountain West. Rogers et al. (2000) provided useful information with the report of 10 taxa from SAM Cave: *Tachybaptus* cf. *T. dominicus* (Least Grebe), *Phasianus colchicus* (Ring-Necked or Common Pheasant), *Troglodytes* cf. *T. troglodytes* (Winter Wren), Corvini, *Ammodramus* sp. (sparrow), *Junco* sp. (junco), *Passerculus* cf. *P. sandwichensis* (Savannah Sparrow), *Parus* sp. (tit), *Vireo* sp. (vireo), and *Asio* cf. *A. flammeus* (Short-eared Owl). The new records from Porcupine Cave add considerably to the diversity of birds known from the region and provide important information on the composition of avian communities in the Rocky Mountains of Colorado. The taxa identified include species reported as fossils for the first time in North America (e.g., the curlew *Numenius madagascariensis* or *N. arquata*), as well as many earlier fossil records than previously known (table 12.1).

The environment surrounding the cave today consists of a mountain park (Herring Park) with grasses, shrubs, and scattered open stands of ponderosa pine, Douglas-fir, and juniper. The lower valley is drained by Herring Creek, and although no riparian forests occur along this creek, there are some moderately large stands of aspen in the vicinity. Many of the avian taxa identified from the cave currently occur in the area either seasonally or year round and represent a diversity of habitats, including wetlands and ponds, alpine tundra, and subalpine forest. Although all these habitats currently occur within a 100-km radius of Porcupine Cave, the avifauna in general suggests that, during the time the fossils accumulated, the environment surrounding the cave was characterized by cooler temperatures and moister conditions than today. Probably within the vicinity of the cave there were more extensive wet meadows or marshes. Many of the avian species recovered from the deposits (e.g., shorebirds, ducks, rails) may have been brought to the cave by avian predators (e.g., eagles, hawks, falcons, owls) that have also been identified from this site. Although the sample size is small, the larger number of

grouse bones from the deposits (table 12.1) is similar to findings by Steadman et al. (1994b) at Rattlesnake Cave, Idaho. Those authors considered roosting raptors as the primary agent for bone deposition in Rattlesnake Cave, where the non-passerine avifauna was dominated by *Centrocercus urophasianus* (Greater Sage-Grouse). A similar interpretation may be applied here.

The avifauna from the early Pleistocene deposits (e.g., Mark's Sink) in particular indicate that wetlands, ponds, marshes, or a combination thereof were located near the cave in association with dry grassland, sagebrush shrubland, and subalpine forest (table 12.1). The presence of sora, phalarope, and gull, taxa not found in the other dated levels, suggests that aquatic and wetland environments may have been more extensive during the early Pleistocene than now. In addition, the abundance of sage grouse bones in these deposits further indicates that large areas of sagebrush shrubland occurred near the cave. Sage grouse are restricted primarily to sagebrush habitats today (Johnsgard, 1973). Species indicative of dry grasslands and tundra include the curlew, longspurs, and rosy-finch, whereas the presence of spruce grouse, blue grouse, and woodpeckers implies that subalpine coniferous forest was located near the site. These interpretations are complicated by the possibility that raptors identified from the cave, including falcon (*Falco* sp.) and owls, may have brought prey items to the cave from a few kilometers away.

Fewer avian fossils are identified from the early middle (~1.0–0.78 Ma) and middle (~780 Ka and somewhat younger) Pleistocene deposits compared to the early Pleistocene ones (table 12.1). However, taxa from the middle Pleistocene are similar to those of the early Pleistocene except that they lack some of the aquatic and wetland species. Only one bone of an unidentifiable goose and three of ducks were recovered from these layers, although the Red-winged Blackbird from the same deposits may also be associated with ponds and wetland environments. Most of the other taxa recovered from the middle Pleistocene are indicative of subalpine forest and shrubland. These differences may be due to excavation sample sizes and could change as new material is recovered from the cave and processed.

Additional fossils from middle to late middle Pleistocene deposits (table 12.1) represent environmental conditions similar to those of the middle Pleistocene with two exceptions. Pinyon Jay and Brewer's Sparrow are more restricted today to lower-elevation shrublands and pinyon-juniper forests, where they currently breed in Colorado. These two species suggest that climatic conditions were warmer than today during the

deposition of sediments in the upper levels of the Velvet Room, though rosy-finch also occur in these levels. It is possible that these sediments accumulated during a relatively warm interglacial interval when more extensive sagebrush shrubland and pinyon-juniper forests may have existed near the cave. Supportive evidence for this interpretation comes from the mammalian record, which includes *Lemmys curtatus* (sagebrush vole), *Cynomys* sp. (prairie dog), and *Mustela nigripes* (black-footed ferret) from the upper levels of the cave deposits (Wood and Barnosky, 1994; Anderson, 1996). Anderson (1996:279), following Barnosky and Rasmussen (1988), suggested that sediments from one room in the cave, the Pit, show that "alternation of fine-grained, light-coloured loess in the upper layers with dark brown, organic-rich clay pellets in the lower layers indicated dry interglacial and wetter glacial intervals, respectively." Uppermost sediments from the Velvet Room have characteristics similar to those of the upper interglacial intervals of the Pit. Lower Velvet Room layers do not have the brown clay pellets, though they are different in character than the upper Velvet Room layers. It is quite probable that long-term climatic cycles were responsible for the diversity of species and environments represented by the fossil vertebrate fauna (Wood and Barnosky, 1994).

Several taxa from the cave represent range extensions from their modern distributions. The presence of a large curlew in the early Pleistocene of Colorado is notable; it is the only Eurasian species in the avifauna. The expansion of wetland habitats during glacial intervals probably facilitated the expansion of this and other aquatic and wetland species during the Pliocene and Pleistocene. Cooler conditions during glacial intervals may also have favored the expansion of alpine tundra and subalpine forests in this part of the Rocky Mountains, allowing for Snowy Owls and Spruce Grouse to reside in Colorado and Wyoming during the Pleistocene. Additional fossils recovered from the extensive deposits at Porcupine Cave will undoubtedly refine these interpretations and continue to add to our knowledge of early and middle Pleistocene avifaunas in Colorado.

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