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Late Pleistocene herpetofauna from two high-elevation caves in the Upper Gunnison Basin, Colorado

Jim I. Mead[1,2,*], Steven D. Emslie[3], and David J. Meltzer[4]

[1]*Mammoth Site of Hot Springs, SD, Box 692, 1800 Hwy. 18 ByPass, Hot Springs, SD 57747*
[2]*Desert Laboratory on Tumamoc Hill, University of Arizona, Tucson, AZ 85745*
[3]*Department of Biology and Marine Biology, University of North Carolina, 601 S. College Road, Wilmington, NC 28403*
[4]*Department of Anthropology, Southern Methodist University, Dallas, TX 75275*

Abstract.—Cement Creek and Haystack caves in Colorado have produced a diverse record of high-elevation late Quaternary mammals. Intermixed with the abundant mammalian remains were rare occurrences of amphibian and reptile fossils reported here. Cement Creek Cave (2860 m elevation) contained the fossils of only a few anurans and a limited number of snakes, whereas Haystack Cave, at a substantially lower elevation (2450 m), contained the fossils of a salamander, a larger number of snakes, and an extensive number of lizard remains, yet no anurans. The 2 faunas are overall distinct in composition, and, although not diverse or abundant in terms of species or number of faunal remains, they provide a rare and exceptional record of a late Pleistocene high-elevation herpetofauna from the Intermountain West.

Resumen.—Las cuevas Cement Creek y Haystack en Colorado han producido un diverso registro de mamíferos de gran altitud del Cuaternario tardío. Entre los abundantes restos de mamíferos, se registraron raros casos de anfibios y reptiles, los cuales reportamos a continuación. En la cueva Cement Creek (2860 m de elevación) se encontraron solo unos pocos anuros y un número limitado de serpientes. Mientras que, en la cueva Haystack, a una elevación sustancialmente más baja (2450 m de elevación), se encontraron una salamandra, una mayor cantidad de serpientes y una gran cantidad de restos de lagartos, pero no anuros. Las dos faunas son distintas en su composición en general y, aunque no son diversas ni abundantes en términos de especies o número de restos de fauna, proporcionan un registro único y excepcional de una herpetofauna de alta elevación del Pleistoceno tardío del oeste intermontañoso.

The Late Pleistocene record of subalpine and alpine amphibian and reptilian (herpetofaunal) communities is poorly understood for greater North America, with the southern Rocky Mountains of Colorado being no exception. Sites with well-preserved mammalian and herpetofaunal fossils in this region are uncommon, but there are the rare occurrences at the high-elevation localities of Porcupine Cave and Snowmass (Ziegler Reservoir; Barnosky et al. 2004, Pigati et al. 2014). To enhance the record of the high-elevation vertebrate communities for the southern Rocky Mountains, a series of 3 caves were investigated in the Upper Gunnison Basin (UGB) of southwestern Colorado (Emslie and Meltzer 2019; Fig. 1).

The UGB is a large (approximately 11,000 km^2 [4250 mi^2]), high-elevation basin that slopes westward from the western flank of the Rocky Mountains to the eastern edge of the Colorado Plateau. Because of its elevation and the surrounding mountains, the UGB is (and has been in the past) marked by a cold, continental climate with bitter winter temperatures and an annual average precipitation of just 25 cm (10 inches) on the basin floor, which increases considerably at higher elevations (Hammerson 1999, Emslie and Meltzer 2019, Andrews et al. 2021). Approximately 30% of annual precipitation today occurs during the late-summer monsoon, with winter precipitation occurring primarily as snowfall. The present-day vegetation is alpine tundra at the highest elevations, grading down through a succession of forested communities. Although the tree species change in elevation in a predictable Rocky Mountain gradient (Fall 1997), the herbaceous communities do not change predictably (Barrell 1969). Late

*Corresponding author: jmead@mammothsite.org

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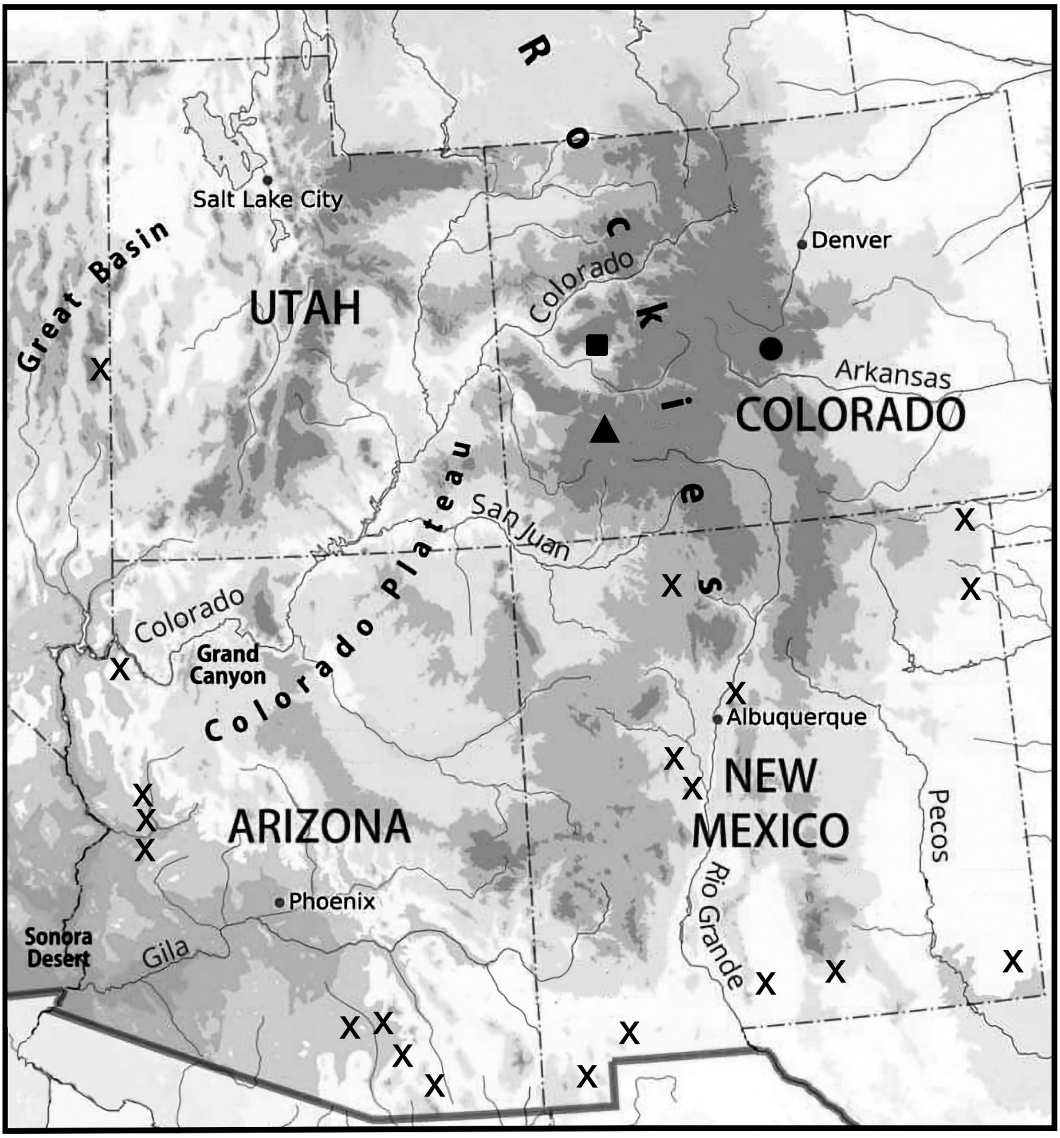

Fig. 1. Map of the greater Southwest, USA, locating Haystack and Cement Creek caves (triangle), Porcupine Cave (black dot), and Snowmass (black square) in Colorado along with the various herpetofaunal localities mentioned in the discussion (X's).

Pleistocene alpine glaciers occurred in the surrounding mountains of the UGB, including the Elk and Sawatch ranges along with the San Juan Mountains to the south (Brugger 2010, Anderson et al. 2020). During the Late Pleistocene, temperatures in the UGB were cooler, with wetter springs and summers and increased winter snows. The upper and lower treelines in the UGB, at approximately 3450 and 2750 m above sea level, respectively, were about 300 to 700 m lower during cooler periods of the Late Pleistocene than they are at present (Fall 1997, Briles et al. 2012, Andrews et al. 2021).

A series of 3 caves from the UGB provide an elevational gradient of Late Pleistocene faunas along the western slope of the Rocky Mountains. (1) Haystack Cave, at 2450 m (8040 ft) elevation, is lowest and currently is in a xeric basin environment. (2) Cement Creek Cave, at 2860 m (9385 ft), and (3) Signature Cave, at

3055 m (10,025 ft), are in higher, cooler, and wetter elevations within the UGB. All 3 caves are within a 60 km (38 mi) distance of each other (Fig. 1). These 3 caves have produced a wealth of information regarding their botanical, avian, and mammalian late Quaternary remains (Emslie 1986, 2002, Emslie et al. 2005, McLean and Emslie 2012, Reynard et al. 2015, Emslie and Meltzer 2019, Andrews et al. 2021). Herpetofaunal species presented here are far rarer, with remains recovered from only 2 of the caves (Haystack and Cement Creek caves), and even in these localities, these remains are infrequent. Nonetheless, given the meager record of high-elevation Late Pleistocene herpetofaunas, they are of interest and presented here.

COLORADO HERPETOFAUNA OVERVIEW

Amphibians, including salamanders (Caudata) along with frogs and toads (Anura), are present in Colorado today. Caudata in Colorado are represented by a single family (Ambystomatidae = mole salamanders) and one genus (*Ambystoma*). *Ambystoma* occurs throughout Colorado from the lowest elevations up to approximately 3660 m (12,000 ft). Today, at least 16 species of *Ambystoma* live across North America (Petranka 1998, Green et al. 2013); however, the systematics within *Ambystoma* are unresolved. *Ambystoma mavortium* (*tigrinum*) is found throughout most of Colorado today, including the UGB (Hammerson 1999). There is discussion regarding the level of molecular and skeletal distinction between *A. mavortium* and *A. tigrinum* (the latter now considered to occur only in eastern USA; Green et al. 2013). *Ambystoma mavortium* is a large-sized, widespread species which can survive in arid regions by undergoing facultative neoteny (retention of larval characteristics such as external gills at sexual maturity; Pedersen 1993). Current species distribution of *Ambystoma* in Colorado would suggest that a UGB fossil is likely *A. mavortium*; however, this taxon could be a more recent immigrant, with Late Pleistocene–age habitats being occupied by other species until recently. Based on current geographic distributions, no other species of *Ambystoma* occurs near the greater Colorado region, with the closest being in eastern Oklahoma and Texas (*A. annulatum*, *A. talpoideum*, *A. texanum*, and *A. tigrinum*) and *A. macrodactylum* in Idaho (Green et al. 2013). The only other salamanders that occur in or near Colorado are the relictual and highly isolated populations of the 2 plethodontids (Plethodontidae) *Aneides hardii* and *Plethodon neomexicanus*, which are found to the south in New Mexico at high mountainous elevations (Degenhardt et al. 1996, Green et al. 2013).

Five families of anurans live in Colorado today (Hammerson 1999). Molecular studies of anurans have caused some splits within various genera and families, and although these taxonomic assignments are controversial, they will be followed here (https://amphibiansoftheworld.amnh.org, accessed August 2020). Within Scaphiopodidae (spadefoot toads) there are several species, including *Scaphiopus couchii*, *Spea bombifrons*, *Sp. intermontana*, and *Sp. multiplicata*. No species of spadefoot toad is extant within the UGB; however, *Sp. intermontana* is found at lower elevations in the northwestern part of the state.

The large genus *Bufo* (Bufonidae; true toads) has been split into several genera. For extant species in Colorado (Hammerson 1999), all bufonids are within the genus *Anaxyrus*: *A. boreas*, *A. cognatus*, *A. debilis*, *A. punctatus*, and *A. woodhousii*. *Anaxyrus boreas* is found geographically nearby and above the elevation of both caves today, and this may also be the case for *A. woodhousii*. The other species within this genus are found in different habitats than those occurring around the caves and adjacent mountains.

The family Hylidae (treefrogs) in Colorado contains *Acris crepitans*, *Dryophytes* (*Hyla*) *arenicolor*, and *Pseudacris triseriata*. *Acris* and *Dryophytes* do not occur near the caves or adjacent mountains today, but *Pseudacris* can be found throughout most of the state from lowlands to above 3670 m (12,000 ft) elevation. The family Microhylidae (narrowmouth toads) in Colorado contains the minute *Gastrophryne olivacea*, which is distributed only in the southeastern-most portion of the state, areas with more grassland and rock-rimmed canyons.

Members within the Ranidae (true frogs) have also seen some taxonomic changes. In Colorado, Ranidae includes *Lithobates* (*Rana*) *blairi*, *L. catesbeianus* (introduced), *L. pipiens*, and *L. sylvaticus*. *Lithobates pipiens* can be found throughout most of the state, well into the mountains along the riparian corridors, meadows, lakes, and glacial kettle ponds, and it is the only ranid extant in the area of the caves today.

Extirpations of select montane populations of *L. pipiens* have been reported (Corn and Fogleman 1984).

Reptiles occurring today in Colorado include turtles (Testudines; not mentioned further here due to lack of fossils in the caves reported here) and squamates (Squamata; lizards and snakes). We adopt here the family-level taxonomy of squamates used by Frost and Etheridge (1989), Gauthier et al. (2012), Pyron et al. (2013), and Zaher et al. (2019), although we recognize the variation within their taxonomic categories. Lizards within the Crotaphytidae include the collared (*Crotaphytus*) and leopard (*Gambelia*) lizards. The Phrynosomatidae are a large and somewhat complex group of lizards (see below) which include *Callisaurus*, *Cophosaurus*, *Holbrookia*, *Petrosaurus*, *Phrynosoma*, *Sceloporus*, *Uma*, *Urosaurus*, and *Uta*. Teiidae include the racerunner and whiptail lizards (*Aspidoscelis; = Cnemidophorus*). Scincidae include skinks, which are otherwise rare in Colorado (*Plestiodon*; Hammerson 1999).

Members of the following snake clades live today in Colorado (Hammerson 1999): Leptotyphlopidae (slender blind snakes [*Leptotyphlops*]), Colubridae (colubrid snakes [*Arizona*, *Coluber*, *Pantherophis*, *Lampropeltis*, *Liochlorophis* (= *Opheodrys*), *Masticophis*, *Pituophis*, *Rhinocheilus*, *Sonora*, and *Tantilla*]), Dipsadidae (dipsadid snakes [*Diadophis*, *Heterodon*, and *Hypsiglena*]), Natricidae (natricine snakes [*Nerodia*, *Thamnophis*, and *Tropidoclonion*]), and Viperidae (rattlesnakes [*Crotalus*]).

METHODS

Haystack Cave overlooks the dry central portion of the UGB, about 150 m (490 ft) above the Gunnison River (now the Blue Mesa Reservoir) that flows across the basin floor. The present vegetation surrounding the cave is dominated by sagebrush (*Artemisia tridentata*), along with the deciduous Gambel oak (*Quercus gambelii*) and Rocky Mountain juniper (*Juniperus scopulorum*). This tube-shaped cave is in Oligocene-age Fish Canyon welded tuff and extends from its entrance only about 12 m (40 ft) into the hillside. Excavations occurred in 1978 (Euler and Stiger 1981, Emslie 1986) and again in 1986/1987 (Nash 1987), with smaller excavation and stabilization work in 1998 (Emslie 2002, Emslie and Meltzer 2019). Twenty-nine radiocarbon ages of vertebrate remains that are from the stratified layers indicate that most of the recovered faunal species date between approximately 24,780 and 15,165 calibrated radiocarbon years before present (cal yr BP; details to be found in Emslie and Meltzer 2019); the herpetofauna reported here fall within this same age range.

Cement Creek Cave is a multichambered cavern within the Paleozoic-age Leadville Limestone. It has a relatively small (1-m-diameter) circular opening that is currently about 3 m above the outside ground surface, which itself is approximately 184 m above the valley floor. Once through the entrance, the cave opens into a small antechamber, from which there are several shafts extending downslope into the mountainside. What appears as the main passageway at present extends from the antechamber about 12 m on a roughly 30° downward angle toward the north, where it then levels out into a small, relatively low-ceilinged inner chamber 3 m in diameter. This inner chamber serves as a topographic "collection point" for sediments and fossils that rolled or washed down the passageway from the entrance and antechamber; it is also a locus of rodent activity, especially of the local bushy-tailed packrat (*Neotoma cinerea*). The herpetofauna reported here comes from this inner chamber. At the height of the most recent Wisconsinan glaciation, the cave was within about 8 km (5 mi) of a terminal glacial lobe (Brugger 2010).

Two excavation seasons (Test Pit 1, 1998; Test Pit 2, 2007) recovered sediments dominated by avian and mammalian remains, including at least 5 species of shrews (Emslie 2002), but some amphibian and reptilian fossils were also recovered. The cave appears to have been used heavily by packrats but also by raptors and by small carnivores (including mustelids) that used it as a den. The recovery of herpetofaunal remains is irregular throughout the various layers, with radiocarbon dates indicating ages from the middle Holocene back to about 46,000 cal yr BP (Emslie and Meltzer 2019). Details and supplementary information about the chronology and vertebrate history from these caves are in Emslie and Meltzer (2019).

Identifications of the herpetofaunal remains from Haystack and Cement Creek caves were made with the aid of the comparative skeletal collection at The Mammoth Site (Hot Springs, South Dakota) and relevant literature sources (as cited in the text). Specimens are curated at the Canyons of the Ancients Visitor Center

TABLE 1. Taxa of herpetofauna from Haystack Cave and Cement Creek Cave listed by skeletal element and stratigraphic level. Specimen numbers are listed in the text under the respective taxonomic descriptions. All Haystack Cave specimens are from test pit K3/4. Abbreviations: Lv = level within excavation unit, TP = test pit.

Location and taxon	Skeletal element	Stratigraphic level (n =)
Haystack Cave		
Ambystoma sp.	Trunk vertebra	Lv9 (1)
Sceloporus sp.	Dentary	Lv6 (2)
Sceloporus sp.	Dentary	Lv8
Sceloporus sp.	Dentary	Lv12 (2)
Sceloporus sp.	Dentary	Lv21
Sceloporus sp.	Dentary	Lv23
Sceloporus sp.	Dentary	Slump
Sceloporus sp.	Maxilla	Lv2
Sceloporus sp.	Maxilla	Lv3
Sceloporus sp.	Maxilla	Lv6
Sceloporus sp.	Maxilla	Lv7
Sceloporus sp.	Maxilla	Lv9
Sceloporus sp.	Maxilla	Lv18
Sceloporus sp.	Maxilla	Slump
Sceloporus sp. small form	Dentary	Lv6
Sceloporus sp. small form	Dentary	Slump Lv7 (2)
Sceloporus sp. small form	Dentary	Back of cave
Pituophis/*Arizona*	Vertebra	Lv14
Pituophis sp.	Vertebra	Lv14
Pituophis sp.	Vertebra	Lv16
Pituophis sp.	Vertebra	Lv19
Pituophis sp.	Vertebra	Lv21
Thamnophis sp.	Vertebra	Lv3
Thamnophis sp.	Vertebra	Lv4 (2)
Thamnophis sp.	Vertebra	Lv10
Thamnophis sp.	Vertebra	Lv22
Thamnophis sp.	Vertebra	Lv22
Cement Creek Cave		
Anaxyrus sp.	Humerus	TP 1: Lv8
Anaxyrus sp.	Humerus	TP 2: Lv8
Anaxyrus sp.	Tibiofibula	TP 1: Lv3
Anaxyrus sp.	Tibiofibula	TP 1: Lv7
Anaxyrus sp.	Tibiofibula	TP 1: Lv8 (2)
Anaxyrus sp.	Tibiofibula	TP 2: Lv15
Anaxyrus sp.	Ilium	TP 1: Lv10
Anaxyrus sp.	Astragalus/calcaneus	TP 1: Lv8
Pituophis sp.	Vertebra	TP 1: Lv10
Thamnophis sp.	Vertebra	TP 1: Lv4 (2)
Thamnophis sp.	Vertebra	TP 1: Lv7
Thamnophis sp.	Vertebra	TP 1: Lv9
Thamnophis sp.	Vertebra	TP 2: Lv10

(Dolores, Colorado). Specimen numbers for Haystack Cave are 2010.14.5GN189.420–457 and 2010.20.5GN189.2087; specimen numbers for Cement Creek Cave are 2003.20.1–20.

All specimens reported here were removed in test pit excavations (Table 1); however, there were different designations for these units, one being numerical test pits including 1 and 2, and the other being an alphabetically labeled system such that K3/4 refers to row K with test pits 3 and 4 (see overview in Emslie and Meltzer 2019, and references within). The referred material below uses the following format—Cave: skeletal element: provenience (level: specimen number). Abbreviations: R = right, L = left, Lv = level, TP = test pit, K3/4 = test pit, NE = northeast test pit. Terminology for the identification of amphibians follows Tihen (1942, 1955, 1958) and Holman (2006) for caudates, and Sanchiz (1998), Holman (2003), Bever (2005), and Gómez and Turazzini (2016) for anurans. Terminology for the squamate osteology predominantly follows Evans (2008) and Gauthier et al. (2012) for lizards, and Auffenberg (1963) and LaDuke (1991) for snakes.

SYSTEMATIC PALEONTOLOGY

CLASS AMPHIBIA

Caudata Scopoli, 1777
Ambystomatidae Gray, 1850
Ambystoma sp. Tschudi, 1838
Salamander

REFERRED MATERIAL.—Haystack Cave: anterior trunk vertebra: K3/4 (Lv 9: 2010.14.5GN 189.426).

DISCUSSION.—The single vertebra has a centrum length (cl) of 2.0 mm. With short transverse processes, a relatively short anteroposterior neural spine, and a high neural arch, the specimen is likely the second (possibly the third) trunk vertebra (Holman 2006) (Fig. 2B). The spinal nerve foramen exposed posterior to the transverse processes indicates that with these above characters, the specimen is consistent with a vertebra of *Ambystoma* and is unlike those found in the large *Dicamptodon* (Dicamptodontidae), the smaller *Taricha* (Salamandridae), and the typically minute, delicate plethodontid species (Plethodontidae; Edwards 1976). From a neotenic life stage, the centrum has a continuous notochord opening.

Conspecific individuals of *Ambystoma* sp. may present differing morphologies that complicate fossil identification. The condition of neoteny within fossil vertebrae can be inferred by well-ossified trunk vertebrae with open notochordal canals (Tihen 1942, 1955, 1958, Holman 1975, Rogers 1985, Holman 2006). Another condition found in the living forms of *Ambystoma* is variation in skull growth due to cannibalistic behavior (e.g., Rose and Armentrout 1976, Pedersen 1993); this morphology has not been evaluated in terms of skeletal identification issues related to each species. Thus, it is questionable that isolated vertebrae, and possibly other skeletal remains of *Ambystoma*, can be satisfactorily identified to species level, given the large variation in individual size and shape of larval and terrestrial mole salamanders. Warm, aquatic habitats that do not support more predatory fish tend to have more abundant neotenic salamanders, while cold, well-oxygenated waters tend to have fewer. Ambystomatids generally metamorphose rather than compete with predatory fish in the cold waters (Rogers 1987).

Anura Hogg, 1839
Bufonidae Gray, 1825
Anaxyrus sp. (*Bufo*) Tschudi, 1845
Toad

COMMENT.—Taxonomy follows *Amphibian Species of the World* (https://amphibiansoftheworld.amnh.org, acccessed January 2022).

REFERRED MATERIAL.—Cement Creek Cave: humeri: TP 1 (Lv 8: 2003.20.5), TP 2 (Lv 8: 2003.20.1); tibiofibulae: TP 1 (Lv 3: 2003.20.2; Lv 7: 2003.20.4; Lv 8: 2003.20.6, 2003.20.8, n = 2), TP 2 (NE, Lv 15: 2003.20.3); ilium: TP 1 (Lv 10: 2003.20.9); astragalus/calcaneus: TP 1 (Lv 8: 2003.20.7).

DISCUSSION.—A single right, fragmented ilium (2003.20.9) was recovered. There is evidence for slight dissolution of bone, likely due to digestion by a predator. The broken ilial shaft is robust and is 14.2 mm long. There is no evidence of a dorsal ilial crest having been present. Portions of the pars ascendens and pars descendens (= dorsal and ventral acetabular expansions) are missing. A remaining portion of the preacetabular zone of the pars descendens indicates that there was minimal expansion. The acetabular fossa is mostly preserved. The tuber superior (= dorsal tubercle and the dorsal prominence) is distinct but not large and positioned predominantly anterior to the acetabular fossa. Although slightly dissolved, there remains evidence that the dorsal prominence was roughened with grooves (character state #4 in Bever 2005). The tuber superior is not inclined; both slopes are gradual and about the same angle—not steep (Tihen 1962, Bever 2005).

Based on modern comparative specimens and Holman (2003), the lack of a dorsal ilial crest indicates that the fossil does not belong to any member within Ranidae. The ilial shaft is distinctly more robust than occurs in either *Spea* or *Scaphiopus*; therefore, the fossil is not within the Scaphiopodidae. The size and robustness of the fossil ilium negates the possibility that it belongs to any hylid or microhylid. Thus, by process of elimination, the fossil ilium is identified as belonging to a bufonid. Bever's (2005) analysis of *Bufo* indicated that there is much interspecific variation within ilial characters, making species-level identifications suspect. His analysis of "*Bufo*" species included what are now those within *Anaxyrus*, *Incilius*, and *Rhinella*, although we are not certain how much this inclusion might change the overriding results. In using Bever's character #4 (surface

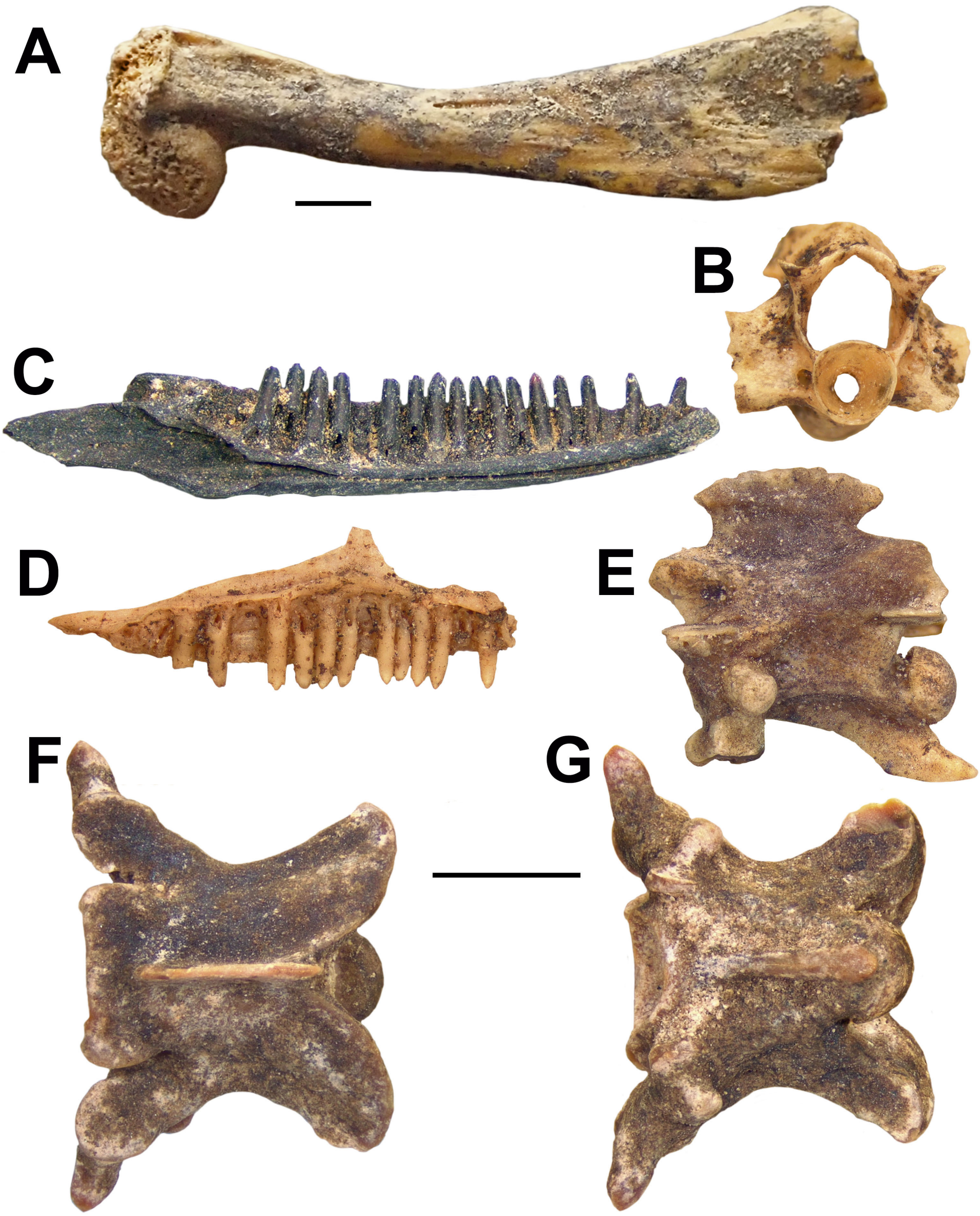

Fig. 2. Illustration of select herpetofaunal species from Haystack and Cement Creek caves. ***A,*** *Anaxyrus* sp. (toad) humerus (lateral view) from Cement Creek Cave (2003.20.1). ***B,*** *Ambystoma* sp. (mole salamander) neotenic vertebra (anterior view) with the open notochordal canal from Haystack Cave (2010.14.5GN189.426). ***C,*** *Sceloporus* sp. (spiny lizard) left dentary (lingual view) (22010.14.5GN189.437). ***D,*** *Sceloporus* sp. left maxilla (lingual view) from Haystack Cave (2010.14.5GN189.441). ***E,*** *Thamnophis* sp. (garter snake) midtrunk vertebra (lateral view, anterior to left) from Haystack Cave (2010.14.5GN189.422). ***F*** and ***G,*** cf. *Pituophis* sp. (bullsnake) midtrunk vertebra (dorsal and ventral view, respectively) from Haystack Cave (2010.14.5GN189.432). Scale bars equal 2 mm.

of dorsal prominence smooth or rough; Bever 2005) and our analysis of our modern comparative collection, it appears that the fossil ilium does not belong to any species of *Incilius* or *Rhinella*. Accordingly, we identify the fossil ilium to be a member of *Anaxyrus*. We agree with Bever (2005) that we cannot use his character #4 to identify the ilium to a particular species within *Anaxyrus*. The robustness and overall size of the fossil ilium is equivalent to that found in *A. woodhousii*, with a SVL (snout–vent length) of ~68 mm. This size of a toad is obtainable in a number of species and therefore is not overly diagnostic; thus, our identification is *Anaxyrus* sp.

A right humerus (2003.20.1; Fig. 2A) has a length of 18.7 mm with a robust diaphysis, a prominent medial crest, and a less prominent radial epicondyle. The ventral crest is present proximally on about half the diaphysis but is not robust. *Spea* and *Scaphiopus* have a relatively large ventral crest that is more than 50% of the diaphysis length; thus, 2003.20.1 is not a scaphiopodid. Hylids have humeri that are typically small with a long (~75% the length) ventral crest; thus, 2003.20.1 is not a hylid. Ranids have a more slender diaphysis (compared to 2003.20.1) and have a slight or absent medial crest with a slight lateral crest. The ventral crest never seems prominent on ranids, except for the shortened yet high crest on the introduced *Rana catesbiana*. Consequently, 2003.20.1 is not a ranid. The ulnar epicondyle (medial) is prominent on both 2003.20.1 and *Anaxyrus*. The medial crest does not appear on examined specimens of *A. cognatus* and is slight on the diminutive *A. debilis*. The medial crest varies by sex in *Anaxyrus*, being more prominent on males. The fossil humerus 2003.20.1 compares closest to a larger, male *Anaxyrus*; however, the species cannot be assigned. The humerus 2003.20.1 and humerus 2003.20.5 (length 21.2 mm with characters of 2003.20.1) are distinctly larger than humeri in the hylids *Pseudacris*, *Acris*, and *Dryophytes* and in the microhylid *Gastrophryne*.

Five tibiofibulae were recovered, all morphologically similar; 2003.20.8 is described to represent the group. The complete tibiofibular is 20.9 mm long and relatively robust in relation to length/width. Tibiofibulae of ranids and hylids are longer (but in some cases much smaller), thinner, and often more delicate than the fossils in this study. In *Spea* and *Scaphiopus*, the sulcus separating the 2 diaphyses at the proximal and distal ends is not pronounced, whereas in the fossil and *Anaxyrus*, the sulcus is relatively deep, making the separation more prominent. Thus, these fossils are identified as belonging to *Anaxyrus*, but we find no characters to permit species-level identification.

CLASS REPTILIA

Squamata Oppel, 1811
Iguania Cuvier, 1817
Pleurodonta Cope, 1864
Phrynosomatidae Fitzinger, 1843
Phrynosomatid Lizard

REMARKS.—The large group of phrynosomatid lizards are often divided into 2 subclades (Wiens et al. 2010, 2012): (1) Sceloporinae (sceloporine lizards): *Sceloporus*, *Petrosaurus*, *Urosaurus*, and *Uta*; and (2) Phrynosomatinae (sand lizards): *Phrynosoma*, *Callisaurus*, *Cophosaurus*, *Holbrookia*, and *Uma*. This latter subclade is divided into 2 groups: (a) *Phrynosoma* and (b) *Callisaurus*, *Cophosaurus*, *Holbrookia*, and *Uma*. All lizard fossils described here are members of Lepidosauria based on the presence of pleurodont tooth implantation (Gauthier et al. 1988, Scarpetta 2021).

Sceloporus sp.
Midsized Spiny Lizard Morphology

REFERRED MATERIAL.— Haystack: dentaries: K3/4 (Lv 6: 2010.14.5GN189.423, 440; Lv 8: 2010.14.5GN189.442; Lv 12: 2010.14.5GN189.428, 444; Lv 21: 2010.14.5GN189.448; Lv 23: 2010.14.5GN189.436; slump back of cave: 2010.14.5GN189.453); maxillae: K3/4 (Lv 2: 2010.14.5GN189.437; Lv 3: 2010.14.5GN189.438; Lv 6: 2010.14.5GN189.441; Lv 7: 2010.14.5GN189.424; Lv 9: 2010.14.5GN189.443; Lv 18: 2010.14.5GN189.431; slump 1c3: 2010.14.5GN189.450).

DISCUSSION.—Fossil specimens described here and within *Sceloporus* sp. small form (below) can be placed within the Phrynosomatidae based on the following dental and tooth-bearing bone characters: (1) constriction of the Meckelian groove, (2) closure of the Meckelian groove without fusion of the infra- and suprameckelian lips, and (3) gracile, minute (yet distinct) tricuspate teeth with unflared tooth crowns (see details in Etheridge and de Queiroz 1988, Bhullar and Smith 2008, Scarpetta 2021).

Specimen 2010.14.5GN189.423 (representing all dentaries here) is a complete right dentary (length of 7.2 mm) with a tooth row of 12 teeth and space for additional 5 teeth. The Meckelian groove is closed (inframeckelian and supra-meckelian lips contact but are not fused) and meets the splenial at the posterior-most fourth tooth. Posterior teeth are wide, straight, and parallel-sided with the posterior 8 teeth weakly tricuspate. Anterior 4 teeth are parallel sided up to a point, not recurved, and fixed to a subdental gutter. The alveolar surface curves dorsally, which gives the posterior portion of the dentary an exaggerated, greater height than the anterior portion. A dentary dorsal curvature is also observed in the other sceloporines (*Urosaurus* and *Uta*) and in the sand lizards, but typically is not as exaggerated, albeit there is much variation (see also Scarpetta 2021). All dentaries in this grouping lack the derived morphology observed in *Phrynosoma* (Mead et al. 1999, Bell et al. 2004a).

Specimen 2010.14.5GN189.441 is a left maxilla (Fig. 2D) and represents all maxillae within this taxon (complimentary left dentary 22010 .14.5GN189.437 shown in Fig. 2C). The bone is complete, including the ascending nasal (= facial) process. The tooth row is 4.9 mm in length, with 16 teeth and space for an additional 3 teeth. The 3 anterior teeth are bluntly pointed at the apex, with the rest of the teeth weakly tricuspate. Teeth are parallel sided and not recurved.

With the above characters and features discussed here and in Scarpetta (2021), the dentaries and maxillae are not members of the Crotaphytidae. The anterior teeth are not the distinctly delicate, highly pointed teeth typical of *Urosaurus* and *Uta*. Morphologically, specimen 2010.14.5GN189.423 most closely resembles one of the smaller to midsized, less robust members within *Sceloporus*; no skeletal characters are known to systematically differentiate all of the various species within this large genus. Although similar in appearance to *S. undulatus* and *S. occidentalis*, 2010.14.5GN189.423 could easily be one of the many other numerous midsized sceloporine species living today in western North America.

Today, midsized species of *Sceloporus* in Colorado include *S. magister* (desert spiny lizard), found in the xeric and low-elevation biotic communities in the southwest corner of the state, and *S. undulatus* (prairie and plateau lizards), found throughout the state up to elevations where ponderosa pine and Douglas-fir montane forest communities occur (Hammerson 1999).

Sceloporus sp.
Small Spiny Lizard Morphology

REFERRED MATERIAL.— Haystack: dentaries: K3/4 (Lv 6: 2010.14.5GN189.439), slump (Lv 7: 2010.14.5GN189.451–452; back of cave: 2010 .14.5GN189.449).

DISCUSSION.—The small, slightly fragmented left dentary (2010.14.5GN189.439) has 14 teeth present, with space for an additional 3; the tooth row is 4.4 mm in length. The distal-most portion is missing, along with the inframeckelian lip; a partial expansion of the suprameckelian lip occurs at tooth 11. The teeth are small and microtricuspate for the posterior teeth and conical for the anterior teeth. All teeth are parallel sided to the apex and not recurved. Teeth and dentary do not show the delicate and minute size observed in *Urosaurus* and *Uta*.

Three dentaries (2 left and 1 right) were recovered in slump deposits in the back of the cave. Tooth row lengths vary from 5.2 to 5.9 mm in length. Two dentaries are charred by fire. Respectively, the tooth rows contain 16 teeth plus space for 4 more, 16 teeth plus space for 5 more, and 18 teeth plus space for 4 more. Teeth are parallel sided, small (but not delicate) and developed into points, slightly oriented lingually for the anterior 30% to 50% of the tooth row, with the posterior teeth being slightly tricuspate. Dentaries, although small, are more robust than in *Urosaurus* and *Uta*.

Given the above observations, the dentaries appear to be from a member of *Sceloporus* and represent a small form similar to the presently extant *S. graciosus* (sagebrush lizard). However, given the number of small extant species that occur near Colorado and the lack of known apomorphies to differentiate these similar species, we hesitate to definitively assign the fossil to the sagebrush lizard but merely imply its similarity to *S. graciosus* and indicate that it is a small species form. *Sceloporus graciosus* is found today throughout western Colorado, including portions of the UGB from semidesert shrublands, oak-grasslands, piñon-juniper woodland, and montane woodlands with ponderosa pine and Douglas-fir (Hammerson 1999), and the fossil is thus a likely contender for this species identification, albeit a number of small species forms live to the south, southwest, and southeast of Colorado (Stebbins 2003).

Serpentes
Colubridae
Pituophis or *Arizona*
Bullsnake or Glossy Snake

REFERRED MATERIAL.—Haystack Cave: midtrunk vertebra: K3/4 (Lv 14: 2010.14.5GN189.429).

DISCUSSION.—Midtrunk vertebra 2010.14.5GN189.429 is complete and relatively small, but not minute. A cotyle length (cl) of 3.5 mm and a neural arch width (naw) of 3.4 mm gives a cl:naw ratio of 1.03, essentially square. The neural spine height is low (0.03 mm) and has a length of 2.6 mm, with weak to no overhangs anteriorly or posteriorly. The accessory processes are oriented transverse to the length of the centrum and are relatively small and blunt (length 0.06 mm). The centrum is round. The parapophysis is minute and distinct from the diapophysis and does not project below the cotyle. There is no paracotylar notch. The neural arch is slightly vaulted, with the zygosphene slightly arched in anterior view. Epizygapophyseal spines are absent, but there are neural arch laminae slightly convex laterally. The hemal keel is low, with little shape and no distinct subcentral ridges.

The above characters indicate that 2010.14.5GN189.429 is not a member of the genus *Hypsiglena* (small, rear-fanged colubrids; characters in Van Devender and Mead 1978, Mead et al. 1984, LaDuke 1991). The fossil also lacks the characters of *Lampropeltis* and *Pantherophis* (Mead et al. 1984, LaDuke 1991). Midtrunk vertebrae of *Pituophis* are often larger than those attained by *Arizona*, but smaller members of *Pituophis* can appear similar to this latter snake (LaDuke 1991). A high neural spine can be found in members of both *Pituophis* and *Arizona* (Mead et al. 1984), while the neural spine is low on the fossil described here. It is unlikely that *Arizona* was present at Haystack Cave during the late glacial at the high elevations of UGB (today it is found in eastern and the southwestern-most part of Colorado), although this does not preclude it from being present in the past. The presence of *Pituophis* is more likely; however, the character states cannot differentiate the two in this case.

Pituophis sp.
Bullsnake

REFERRED MATERIAL.—Cement Creek Cave: midtrunk vertebra: TP 1 (Lv 10: 2003.20.14). Haystack Cave: midtrunk vertebrae: K3/4 (Lv 14: 2010.14.5GN189.429; Lv 16: 2010.14.5GN189.430; Lv 19: 2010.14.5GN189.432; Lv 21: 2010.14.5GN189.447).

DISCUSSION.—All midtrunk vertebrae are from nonjuvenile and medium-sized snakes; none represent large individuals. None of the vertebrae are extremely small, nor do they show the morphology of leptotyphlopid snakes or *Diadophis*, *Tantilla*, or *Opheodrys*, and none have the cl:naw ratio or morphology to indicate that they belong to *Coluber*, *Masticophis*, or other snakes with a long centrum (see discussion in LaDuke 1991).

From Cement Creek Cave, a fragmented midtrunk vertebra (2003.20.14) shows dissolution of the extremities. The vertebra cl = 6.2 mm and naw = 5.3 mm, which result in a cl:naw ratio of 1.17. The neural spine is damaged just above the neural arch but did not occupy the full length of the arch. A strong subcentral ridge is present on 2003.20.14 and similar to species of *Pituophis*, but the vertebra is not as robust as typical on forms observed in *Pantherophis* (see discussion in LaDuke 1991, Head et al. 2016). The paradiapophyses are eroded and the cotyle is large and round. The neural arch is tall, with the accessory processes largely removed, possibly via prey consumption. The hypapophysis is slightly eroded and gladiate in form. Character features of Auffenberg (1963) and LaDuke (1991) are used to identify this and other similar specimens as *Pituophis* (see representative specimen in Fig. 2F and 2G from Haystack Cave). No specimens showed all the characters described by these authors that would permit an identification to species.

Natricidae
Thamnophis sp.
Garter Snake

REFERRED MATERIAL.—Cement Creek Cave: midtrunk vertebrae: TP 1 (Lv 4: 2003.20.17, n = 2); (Lv 7: 2003.20.19); (Lv 9: 2003.20.11); TP 2 (Lv 10: 2003.20.18). Haystack Cave: midtrunk vertebrae: K3/4 (Lv 3: 2010.14.5GN189.421; Lv 4: 2010.14.5GN189.422, n = 2; Lv 10: 2010.14.5GN189.427; Lv 22: 2010.14.5GN189.435, 2010.14.5GN189.422, n = 2).

DISCUSSION.—We use a Haystack Cave specimen, 2010.14.5GN189.422 (Fig. 2E), to represent all fossil specimens within this taxon; cl = 4.0 mm, naw = 2.4 mm, and cl:naw ratio = 1.66, indicating that the vertebra is relatively long versus wide. The cotyle is oval and exhibits paracotylar notches on each side. The base of the cotyle is flattened, and there are strong ventrolateral cotylar processes with distinct paracotylar foramina. Parapophyses are prominent but do not extend anterior to the cotyle. Accessory processes extend beyond prezygapophyseal facets. Subcentral ridges are evident with subcentral grooves with minute foramina. There are no epizygapophyseal spines. The neural arch is somewhat dorsoventrally flattened.

The specimens are not small vertebrae as found in *Storeria* or *Virginia*, and they do not represent *Neonatrix* (following discussion in Mead and Steadman 2017). Vertebrae of *Thamnophis* are typically elongate versus the more squared morphology as in *Nerodia* (discussions in Auffenberg 1963, Mead and Steadman 2017). Thus, these specimens are identified as representing *Thamnophis*. We did not find any characters that permit species identification.

Genus et Species Indeterminate

REFERRED MATERIAL.—Cement Creek Cave: caudal or highly fragmented midtrunk vertebrae: TP 1 (Lv 7: 2003.20.20; Lv 36: 2003.20.16; Lv 39: 2003.20.10), TP 2 (2003.20.12–13). Haystack Cave: caudal or highly fragmented midtrunk vertebrae: K3/4 (Lv 18: 2003.20.457; Lv 21: 2003 .20.434); Strat II (Lv 7: 2010.20.5GN189.2087).

DISCUSSION.—These specimens are either too fragmented or do not have morphological characters to permit further, more detailed identifications.

DISCUSSION AND CONCLUSIONS

Cement Creek and Haystack caves have produced a diverse record of high-elevation, late Quaternary mammals (Emslie 1986, 2002, Emslie and Meltzer 2019). Intermixed with the abundant mammalian remains were the rare occurrences of amphibian and reptile fossils reported here. Cement Creek Cave contained only a few anurans and a limited number of snakes, whereas Haystack Cave, at a lower elevation, contained a salamander, a larger number of snakes, and an extensive number of lizard remains, yet no anurans. The 2 faunas are overall not similar in composition, and, although not diverse or abundant in terms of species or number of faunal remains, they provide a rare and exceptional record of a Late Pleistocene, high-elevation herpetofauna from the Intermountain West.

Fossil forms of *Ambystoma* are not overly common in the southern portion of the Intermountain West, including Colorado. There are only 4 Pleistocene-age localities in Colorado that report the recovery of *Ambystoma* (Fig. 1). The oldest of these localities is Mark's Sink, within Porcupine Cave, which is situated at ~2900 m (9515 ft) elevation. Mark's Sink produced only a single trunk vertebra (identified as Ambystomatidae) and is presumed to date to the Blancan North American Land Mammal Age (NALMA; which may be latest Pliocene or earliest Pleistocene; Barnosky et al. 2004, Bell et al. 2004a, 2004b). The Hansen Bluff locality in San Luis Valley is assigned to the late Irvingtonian NALMA and contains abundant *Ambystoma* (as *A. tigrinum*; Rogers 1985). Specimens were recovered from a number of localities (contents from auger cores and open-air sites) within San Luis Valley, and the species inhabited varying climatic regimes during the Irvingtonian, ranging from warm and dry interglacial deposits to cool and wet glacial deposition; there was no evidence of neotenic forms (Rogers 1985, Rogers et al. 1992). The Snowmass fossil site produced an astonishing 22,000 *Ambystoma* (as *A. tigrinum*) specimens representing over 500 individuals dating from Marine Isotope Stages 6 to 4 (MIS; 141,000 to 55,000 yr BP; Rancholabrean NALMA) and representing glacial through interglacial climatic episodes (Mahan et al. 2014, Pigati et al. 2014, Sertich et al. 2014). Both terrestrial and neotenic morphologies were recovered from this site, but none were correlated to the various marine isotope stages. The age of the neotenic *Ambystoma* sp. specimen from Haystack Cave is approximately 21,500 cal BP, which was during a glacial climate regime. *Ambystoma mavortium* occurs in the valley region today.

Ambystoma fossils are found in herpetofaunas to the south in Arizona, New Mexico, and northern Mexico and are reviewed in Darcy et al. (2022) and Mead (2022). Although Pleistocene herpetofaunas are reported west of the UGB in Utah and the Great Basin of Nevada, no salamanders were recovered in those regions (Mead and Bell 1994). Pleistocene herpetofaunas are not reported from northern Colorado or Wyoming, where faunas are dominated by mammalian and avian taxa. Although salamanders appear to be rare in the Late Pleistocene environments recorded in the various cave and packrat midden deposits, this may reflect a bias in fossil collection, recovery methodology, and what is analyzed.

Anurans living today in the Intermountain West are diverse and relatively abundant, with 17 taxa in Colorado; conversely (as expected), the higher elevations (Rocky Mountains) contain fewer species (figure 2.6 in Hammerson 1999). The recovery of just *Anaxyrus* (toad) is predicted, given the distribution of living species (*A. boreas*, *A. woodhousii*), but unfortunately the few specimens recovered did not lend themselves to a species identification. Given the high-elevation location of both caves, especially Cement Creek Cave, occurrences of the minute boreal chorus frog (*Pseudacris maculata*) were expected, but none were recovered. That could, of course, simply be a function of preservation or sampling.

Lizards and snakes are common today throughout Colorado and the Rocky Mountains; as expected, fewer species occur in the higher elevations (in contrast with those in the drier, typically higher elevations to the west of the mountains) and in the somewhat wetter prairie habitats in the eastern region. The presence of the spiny lizard fossils is expected in the 2 caves, given the present low diversity of lizards in the immediate region. The limiting factor during the full- and postglacial period was the cold and possibly dry climate. A taxon likely to have inhabited the UGB at that time could have been the horned lizard, *Phrynosoma*. Although the fossils recovered could not be identified to species, the specimens clearly do not have the morphological traits of any species of *Phrynosoma*.

The recovery and identification of the snakes *Thamnophis* and *Pituophis* are expected based on the living species found in the UGB and higher elevations of the Rocky Mountains. The faunal record here implies that during the glacial, postglacial, and early Holocene the lizard and snake diversity was distinctly low.

The recovery of distinct herpetofaunas from 2 caves in the UGB proves to be important for the description of the local salamander, anuran, lizard, and snake taxa during the full-glacial, postglacial, and early Holocene for the Colorado Rocky Mountain region. The faunal list from the 2 caves discloses differences in taxa, which are likely due to the elevation contrasts and possibly due to the mode of prey capture (avian taxa) and taphonomy of the cave deposits (Emslie and Meltzer 2019). The herpetofaunas recovered also raise the hypothesis that during the full- and postglacial times in higher elevations of the Intermountain West, faunal compositions were relatively sparse in species diversity. Based on the diversity of species available today throughout the Intermountain West (Stebbins 2003), there are few taxa that would have tolerated the cold and surely harsh near-glacial environments. This observation is in contrast with the varying environments and changing biotic communities experienced in the lower elevations throughout the region (see discussions and species lists in Betancourt et al. 1990 and Mead 2005). This inference needs to be tempered by the fact that few high-elevation herpetofaunas have been reported from the Intermountain West; hence, we recommend that future research focus on faunas near glacial environments during the late glacial period. This approach should be taken in specific areas such as in the Great Basin (e.g., Snake Range, eastern Nevada), Colorado Plateau, northern Rocky Mountains (e.g., Wyoming, Montana), and mountainous regions from Texas/New Mexico to northern Mexico (Sonora and Chihuahua).

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