LATE PLEISTOCENE AND HOLOCENE *BISON* OF THE COLORADO PLATEAU

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ABSTRACT—Fossils of *Bison* (bison) are scarce on the Colorado Plateau, especially in and around the Greater Grand Canyon Region. Because of poor preservation and collection biases in the region, various resource managers have erroneously designated bison a nonnative and human-(re)introduced species. This decision directly impacts an extant herd of approximately 400 bison that periodically meander onto Grand Canyon National Park lands from neighboring U.S. Forest Service and State of Arizona lands. We re-examined and verified paleozoological museum specimens of this large mammal confirming a prehistoric and early historic presence of *Bison* on the Colorado Plateau. Our findings indicate that *Bison bison* should be considered a native species on the Colorado Plateau because they have a nearly continuous record of inhabitance in the region. This record is supported by 74 *Bison*-bearing fossil, subfossil, and historical localities since the latest Pleistocene.

RESUMEN—Los fósiles de *Bison* (bisontes) son escasos en la meseta del Colorado, especialmente dentro y alrededor de la región del Gran Cañón. Debido a la pobre preservación de los fósiles y parcialidad en las colecciones de la región, varios administradores de recursos naturales han denominado equivocadamente bisontes como especies exóticas e introducidas por humanos. Esta decisión impacta directamente a la población actual de cerca de 400 bisontes que a veces traspasan a los terrenos del Servicio Forestal de E.E.U.U. y del Estado de Arizona, hasta los terrenos del Parque Nacional del Gran Cañón. Re-examinamos y verificamos especímenes paleozoológicos de museos de este gran mamífero, confirmando la presencia prehistórica e histórica temprana de *Bison* en la meseta del Colorado. Nuestros resultados indican que *Bison bison* debe ser considerado como especie nativa en la meseta del Colorado por su casi continuo registro de habitación dentro de la región. Este record es respaldado por 74 fósiles y subfósiles relacionados con *Bison,* y por localidades históricas desde el Pleistoceno tardío.

Perhaps no other extant animal in North America possesses the cultural, spiritual, ecological, economic, political, and natural history attributes that are emblematic of the North American bison (*Bison bison;* Artiodactyla, Bovidae, Bovini; Isenberg, 1997; Sanderson et al., 2008). Certainly, no other animal boasts the story of surviving the brink of extinction twice. This story does not stop at the North American plains subspecies (*Bison bison bison*), but it also applies to the North American woods bison subspecies (*Bison bison athabascae*) along with the European bison species (*Bison bonasus;* wisent). First, *Bison* survived the megafaunal extinction at the end of the Pleistocene approximately 11,700 calendar years Before Present (cal yr BP) and, in North America, the genus outlived mammoths (*Mammuthus*), mastodons (*Mammut*), horses (*Equus*), ground sloths (*Megalonyx* et al.), and other megafauna while coexisting with early Americans (Paleoindians; Koch and Barnosky, 2006). Second, *Bison* survived the threat of Americans of European descent, who purposefully hunted the bison nearly to extinction, during the late 1800s Common Era (Hornaday, 1889).

The most recent comprehensive analysis of *Bison* distribution in continental North America illustrates an apparent geographic 'gap' of bison records for much of the arid Southwest, especially on the Colorado Plateau (CP; Mc Donald, 1981; Fig. 1). In the western United States, there are well-documented occurrences of Quaternary-aged *Bison* in physiographic provinces neighboring the CP, such as the Great Basin (Jennings, 1978; Scott and Cox, 2008), southern and middle Rocky Mountains (McDonald, 1981), Wyoming Basin (McDonald, 1981), Arizona deserts (Agenbroad and Haynes, 1975; Wolff, 2013), Bonneville Basin (Madsen et al., 2001), and Rio Grande Rift basin (Harris, 2014).

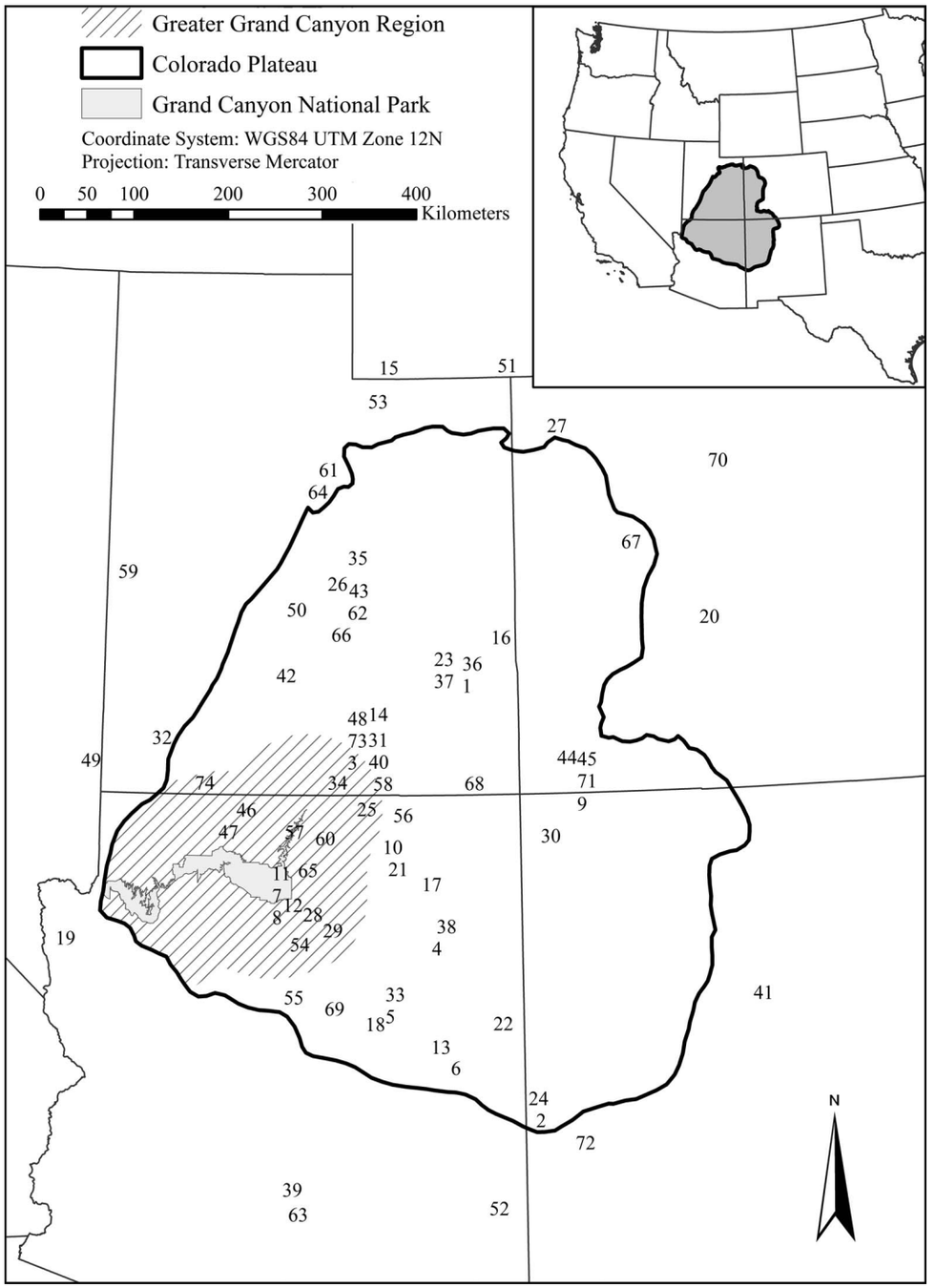

Fig. 1—Map of *Bison* localities (placement is approximate) on the Colorado Plateau (CP, heavy line) and surrounding region. Locality numbers refer to Table 1. Hashed line represents our definition of the Greater Grand Canyon Region (GGC, see Materials and Methods section) surrounding Grand Canyon National Park (GCNP, shaded area).

In recent years, bison from Arizona's House Rock Valley in Arizona have dispersed onto the Kaibab Plateau on the North Rim of the Grand Canyon National Park (NP). Resource managers subsequently questioned the nativity of *Bison* on the CP and concluded, from lack of evidence and limited tangential environmental assessments (Reimondo, 2012; Huffer, 2013), that bison are not native to the area. These prior studies made no examination of specimens in collections but relied upon published literature. Thus, it is necessary to complete a comprehensive assessment of unpublished accounts of *Bison* remains from paleontological and archaeological sites that are preserved in local museum collections.

Here, we synthesize the paleontological and archaeological localities known to contain *Bison* from the Grand Canyon and the surrounding CP along with a few just off

the plateau for adjacent references. Our data set includes published and unpublished accounts and unstudied museum specimens along with those records archived in database systems that have recently emerged. Our goal is to address two main questions: 1) when and 2) where did *Bison* occur on the CP, especially within the Grand Canyon NP and the Greater Grand Canyon Region (as defined in Materials and Methods)? We address these questions by assessing, and in some cases describing, museum specimens of *Bison* from 74 localities on and around the CP (Table 1; Fig. 1). Details about each locality are in the thesis by Martin (2014); we provide only pertinent data herein.

Background—Today, there are two, albeit disputed, subspecies of *Bison* (Cronin et al., 2013): 1) *Bison bison bison* are historically found in the Great Plains and elsewhere throughout much of North America, and 2) *Bison bison athabascae* are historically found north of 49°N latitude in Canada and Alaska. This project does not address subspecies or species but focuses on the animal at the generic level. In all, *Bison bison, Bison antiquus,* and *Bison latifrons* have been reported on the CP and in the surrounding provinces (Table 1).

The historical chronicle of bison in the Southwest is complex and confusing. Northern Arizona has scarce historical records, in general, but the Spanish reported a small herd of *Bison* in the 16th century in east-central New Mexico and adjacent to the CP (Reed, 1952). Native Americans in the 1200s AD and earlier created pictographs and petroglyphs on the walls of Kanab Creek near Kanab, Utah (among other places; Malotki and Wallace, 2011). However, the ideas, memories, and thoughts that inspired these renderings could conceivably have travelled great distances and well beyond the actual zoogeographic distributions, which brings into question the idea that the pictographs and petroglyphs represent local occurrences of bison. A few unrelated, documented occurrences confirm that bison frequented the CP near the Greater Grand Canyon Region in small but self-sustaining herds that most likely had relatively large home ranges to endure the low carrying capacity of the region (Seager et al., 2007).

In 1905, Charles J. "Buffalo" Jones brought bison to the Kaibab Plateau on the North Rim of the Grand Canyon NP (Hoffmeister, 1986) and crossbred them with *Bos taurus* to create a hardy livestock animal he called "cattelo." In 1906, when Congress established the Grand Canyon Game Preserve, they listed bison as one of the wildlife species that should be maintained on the Kaibab Plateau (unpublished report to U.S. Congress, Protection of Wild Animals in the Grand Canyon Forest Preserve). The Kaibab Plateau was described as "ideal for buffalo [*Bison*], deer and other wild game" and was "to be recognized as a breeding place therefore" (Wakeling, 2006:25). Most importantly, "the Preserve was created on 28 November 1906 by President Theodore Roosevelt and is still in effect. It predates the establishment of the [Kaibab] National Forest [in 1909], Grand Canyon National Park [in 1919], and the Arizona Game and Fish Commission [in 1913]" (Wakeling, 2006:25). In 1909, these bison were relocated east to the House Rock Valley (Marble Platform) because of the creation of the Kaibab National Forest when C.J. Jones moved all but 15–20 animals out of the area. The 15–20 remaining bison became property of James T. "Uncle Jim" Owens and, by 1927, the herd had increased to 98 individuals and was purchased by the State of Arizona via the Arizona Game and Fish Department. Over the past half-century, introduced 'purebred' *Bison bison* from Oklahoma and Montana have been added to the bison herd to improve its natural resilience (see discussions in Hoffmeister, 1986; Wakeling, 2006).

Throughout the Holocene, *Bison* abundances spatially varied over most of North America possibly because of hunting and intraspecific competition; yet, the population steadily increased in the Great Plains until European contact when their abundance probably reached their apex (Flores, 1991). This increase in bison might have occurred because of a few conditions including limited trophic-equivalent competition (Flores, 1991); reduced abundance and diversity of presumed predators since the Pleistocene extinction of the dire wolf (*Canis dirus*), American lion (*Panthera atrox*), and the giant short-faced bear (*Arctodus simus;* Flores, 1991); and cooler, wetter climate conditions, which are favorable for grass growth (Wisely et al., 2008; Craine, 2013; Craine et al., 2013). Thus, the observations made by early western explorers (Hornaday, 1889) are likely misleading or at least poorly representative of *Bison* abundance.

Furthermore, earlier in the Holocene, *Bison* were less abundant in the Great Plains and were intermittently present in the Southwest (Broughton et al., 2008). There are potentially multiple factors contributing to the seemingly poor fossil record of *Bison* during the Late Pleistocene and Holocene on the CP. Yet, the region is incompletely studied by Quaternary paleontologists and zooarchaeologists compared with the neighboring provinces, most likely because of its remoteness.

Materials and Methods—The Colorado Plateau is an immense physiographic province between the Colorado Rocky Mountains and the Great Basin Desert (Blakey and Ranney, 2008). The Grand Canyon is defined as the geological gorge that incises the Colorado Plateau (Ranney, 2012) and is immediately surrounded by Grand Canyon NP. We define the Greater Grand Canyon Region as the ecosystem of Grand Canyon NP adjacent to the Colorado River corridor and the plateaus immediately rimming the Grand Canyon gorge. This includes the Coconino, Hualapai, Kaibab, Kanab, Uinkaret, and Shivwits plateaus and the Marble Platform. Thus, we also extend the Greater Grand Canyon Region to approximately 80 km beyond the borders of Grand Canyon NP to encompass the habitats of each plateau (Fig. 1).

TABLE 1—Summary table of *Bison* localities from the Colorado Plateau region. Key refers to number and location in Figure 1. Mean age in calendar years Before Present (cal yr BP) calibrated by IntCal13 (Reimer et al., 2013). References other than primary literature include GRCA collection (Grand Canyon National Park collections), MNA (Museum of Northern Arizona), AZSite (Arizona's Cultural Resource Inventory), NeotomaDB (Neotoma Paleoecology Database), and NeoMap (Neogene Mammal Mapping Portal). "—" indicates no data. Empty cells indicate no information is applicable.

Key	Locality name	Database reference	Mean age (cal yr BP)	Cited age	Dating method	References
1	The Neck[a]	42SA8502	435	Common Era (AD) 1235–1415; AD 1425–1655; AD 1425–1655; AD 1485–1795	Pollen and charcoal	Osborn et al., 1995
2	Ada Mesa[a]	NA20657 Lots 50 & 52	1,100	Georgetown/ San Francisco AD 600–700+; Tularosa AD 1100+ (Mogollon Culture)	Radiocarbon, lithics, and ceramics	—
3	Alcove Spring	42SA8512	453	AD 1345–1650	Pollen and charcoal	Osborn et al., 1995
4	Awatovi[a]	NeotomaDB 5910; NeoMap 2332	850	250–1,450 cal yr BP		Montgomery et al., 1949; Lawrence, 1951; Agenbroad and Haynes, 1975
5	AZ J:14:356[a]		225	0 to 450 cal yr BP	Firepit charcoal	AZSite
6	AZ P:8:3[a]		1,325	1,200–1,450 cal yr BP	Lithics and ceramics	AZSite
7	Mather Campground	B:16:0461	50	50 ± 30 yr	*Bison* phalanx	This study
8	B:16:105	GRCA 69396	1,050	927 cal yr BP; 1000 yr BP (lithics)	*Bison* lipids on ceramics	Downum et al., 2011
9	Badger House	NeotomaDB 1453; NeoMap 1268	814	650–1,100 yr BP	^{14}C on unknown	Hayes and Lancaster, 1975
10	Badger Spring	MNA.Loc.112-0; MNA Ariz D:5:13; NA10924	10,000	7,500–9,500 yr BP	Lithic technology	Hesse et al., 1999; MNA collection
11	Battleship Rock		12,000		Faunal assemblage (*Equus* sp.)	GRCA collection
12	Beamer's Cabin	AZ C:13:0004 GC	555	410–700 cal yr BP	Association of ceramics	Jones, 1986; Huffer, 2013
13	Bear Ruin	AZ P:16:1	625	550–700 cal yr BP	Ceramics	Haury, 1940; Agenbroad and Haynes, 1975; Lightfoot and Feinman, 1982
14	Bechan Cave	NAU QSP Site 872; GLCA Accession 81	15,182	11,670 ± 300; 13,505 ± 580 yr BP	*Mammuthus* dung	Mead and Agenbroad, 1992; Kropf et al., 2007
15	Bessie Bottom Site	48UT1186; NeotomaDB 4810	985	910 ± 80; 1,170 ± 60 yr BP	—	McKern, 1988

TABLE 1— Continued.

Key	Locality name	Database reference	Mean age (cal yr BP)	Cited age	Dating method	References
16	Bison Alcove	42GR538 (ARCH 115); MNA.Loc. 9144; NeotomaDB 6290; NeoMap 2958	445	355 ± 60; 405 ± 65 yr BP	*Bison* horn and hoof	Mead et al., 1991
17	Black Mesa[a]	D:11:2062; D:7:0713; NeotomaDB 6010 & 5980	1,302	885 ± 72; 1,673 ± 117 cal yr BP	—	Leonard, 1989
18	Canyon Diablo Dam	NA8793.Lot.1 #7136	975	Pueblo II	—	—
19	Catclaw Cave	AZ F:2:1(ASM)	7,225	12,000 yr BP–1500 AD	*Bison bison* with assorted fishes associated with lithics and ceramics	AZSite
20	Cement Creek Cave	—	22,585	43,330 ± 760;1,120 ± 40 yr BP	*Marmota flaviventris*	Emslie, 2002
21	Charley Day Spring	NA1898; MNA.Loc. 149-1	14,000	Rancholabrean	Faunal assemblage	MNA collection; Lindsay and Tessman, 1974; Agenbroad and Haynes, 1975
22	Cottonwood Seep Spring[a]	NA14674.Lot.955 and Lot.985 & GSPS6	975	Pueblo II	Lithics	MNA collection
23	Cowboy Cave	45WN420; NeotomaDB 9761; NeoMap 2048	14,519	11,020 ± 180; 13,040 ± 440 yr BP	*Bison* dung	Hansen, 1980; Lucias, 1980; Mead and Agenbroad, 1992
24	Coyote Creek	NA14064	750	Tularosa phase of Anasazi (Pueblo III)	Lithics and buildings	MNA collection
25	Dust Devil Cave	NA7613.Lot. 1066.A9V6; MNA.UT:V: 13:160	975	Kayenta culture (Pueblo II)	Ceramics	—
26	Ephraim (Witch's Knoll)	NeotomaDB: 7683	850	664 ± 6; 1020 ± 22 cal yr BP	—	Gillin and Allen, 1941
27	Fort Davy Crockett	5MF605; NeotomaDB 5210; NeoMap 1165	490	50 ± 1; 927 ± 3 cal yr BP	—	Sharrock, 1966; Walker, 1983
28	Furnace Flats	AZ C:13:0010 GC	995	AD 641–1270	Association of ceramics	Jones, 1986; Huffer, 2013
29	Grand Falls	MNA V8301 Loc.1104	50	50 ± 30 radiocarbon years	*Bison* rib head	This study
30	Gray Water Wash	MNA.Loc.358-0	14,000	Rancholabrean	—	—

TABLE 1—Continued.

Key	Locality name	Database reference	Mean age (cal yr BP)	Cited age	Dating method	References
31	Grobot Grotto	NAU QSP Site 878; GLCA Accession 82	27,384	18,528 ± 137; 33,540 ± 2836 cal yr BP	*Bison* dung	Mead and Agenbroad, 1989, 1992; Withers and Mead, 1993
32	Hamblin Springs	NeoMap 6329	5,850	Holocene	—	—
33	Homolovi I;	AZ J:14:3; MNA AZ J:14:8; NA952	575	Pueblo IV (AD 1300–1450)	Lithic technology and ceramic styles	AZSite
34	Hooper's Hollow	NAU QSP Site 873; GLCA Accession 82	22,783	22,783 ± 405 cal yr BP	*Bison* dung	Mead and Agenbroad, 1989, 1992; Withers and Mead, 1993
35	Huntington Reservoir Sinkhole	NeotomaDB 5737; NeoMap 1953	12,668	12,668 ± 296 yr BP	*Mammut* bone amino acid	Miller, 1987; Gillette and Madsen, 1992
36	Island in the Sky	—	975	Pueblo II	Carving styles	—
37	Jim Walter's Cave	—	14,519	11,020 ± 180; 13,040 ± 440 yr BP	Associated *Bison* dung in Cowboy Cave	Lucias, 1980
38	Keams Canyon	—	14,000	Rancholabrean	—	Hay, 1927; Lindsay and Tessman, 1974; Agenbroad and Haynes, 1975
39	Las Colinas	—	575	Hohokam (Pueblo IV)	—	Johnson, 1974; Agenbroad and Haynes, 1975; Teague and Deaver, 1989
40	Mammoth Alcove	NAU QSP Site 875; GLCA Accession 82	20,082	16,630 ± 280 yr BP	*Mammuthus* dung	Mead and Agenbroad, 1992
41	Martinez Gravel Pit	NeotomaDB 6073	61,655	13,341 ± 30; 110,000 cal yr BP	Bounding formations	Lucas et al., 1988; Smartt et al., 1991
42	Marysvale	NeotomaDB 7682	978	603 ± 37; 1379 ± 12 cal yr BP	Unspecified remains	Gillin and Allen, 1941
43	Mastodon Sinkhole	NeoMap 6315; 42EM231V	14,000	Rancholabrean	Faunal assemblage	—
44	Mesa Verde site 866	NeoMap 1286; NeotomaDB 5320	750	778 ± 18; 856 ± 37 cal yr BP	—	Anderson, 1966
45	Mesa Verde site 875	NeoMap 1284; NeotomaDB 5318	975	856 ± 37; 927 ± 3 cal yr BP	—	Anderson, 1966
46	Kanab Creek	NA8960. NA9074.Lot.2	1,075	850–1300 cal yr BP	—	GRCA collections
47	Mt. Trumbull[a]	NA9074 S-213; MNA.AZ.B:1:23	975	850–1100 cal yr BP	—	MNA collections
48	Oak Haven	GLCA Accession 82; NAU QSP Site 881	11,958	9,180 ± 100; 11,690 ± 120 yr BP	*Quercus gambelii*	Mead and Agenbroad, 1989, 1992; Withers and Mead, 1993

TABLE 1—Continued.

Key	Locality name	Database reference	Mean age (cal yr BP)	Cited age	Dating method	References
49	O'Malley Shelter	NeoMap 2774; NeotomaDB 6162	6,739	7,100 ± 190 yr BP	Charcoal	Fowler et al., 1973
50	Pharo Village	NeoMap 2848; Netoma 6191	681	760 ± 80 yr BP	Wood	Marwitt, 1968
51	Pine Springs	NeotomaDB 4820; 48SW101	8,560	7,695 ± 195 yr BP	Bone collagen	Sharrock, 1966; Frison, 1978
52	Point of Pines	NeoMap 2236 & 2242; NeotomaDB 5866	573	543 ± 28; 595 ± 35 cal yr BP	—	Stein, 1963; Agenbroad and Haynes, 1975
53	Porcupine Cave	NeotomaDB 7680	542	510 ± 75 yr BP	*Ursus americanus* bone	Heaton, 1988
54	Red Horse Wash[b]	NA9528.Lot.4 & Lot.1 (NA 5164)	975	Cohonina/ Anasazi/ Archaic (Pueblo II)	Ceramics	MNA collections
55	Ridge Ruin		750	Hohokam (Pueblo III)	Lithics	Agenbroad and Haynes, 1975
56	Sand Dune Cave[b]	NA7523.Lot. 133:2183 (MNA.UT.V:13 74)	5,650	Navajo or Basketmaker I/ III	—	MNA collections
57	Sandblast Cave	NeoMap 4875; NeotomaDB 7710	13,704	13,110 ± 680 yr BP	Associated *Oreamnos* dung	Emslie, 1987, 1988; Mead and Agenbroad, 1989, 1992
58	Shrub Ox Alcove	GLCA Accession 82; NAU QSP Site 882	15,003	12,690 ± 180 yr BP	*Quercus* twig with *Bison* dung associated	Mead and Agenbroad, 1989, 1992; Withers and Mead, 1993
59	Smith Creek Cave	NeotomaDB 4684; 26WP46	27,267	Reddish-Brown Silt Zone (12,600–35,000 yr BP)	^{14}C on unknown	Bryan, 1979; Mead et al., 1982, 1992
60	Smith Tank Site	CC:5:6	675	1275 AD (Pueblo III)	Ceramics	Woodson, 2007
61	Smoking Pipe	NeotomaDB 6363; 42UT150	621	640 ± 110 yr BP	*Bison bison* bone	Billat, 1985
62	Snake Rock Village	NeoMap 2851; NeotomaDB 6194	736	1,500 ± 95 yr BP	Wood	Aikens, 1967
63	Snaketown	—	1,433	835 ± 109; 1,799 ± 342 cal yr BP	Ceramics	Haury, 1965; Agenbroad and Haynes, 1975
64	Spotten Cave	42UT104, NeotomaDB 6358	684	730 ± 90 yr BP	—	Cook, 1980
65	Stanton's Cave[c]	C:5:3; NAU QSP Site 9121; GRCA Accession 4597; NeotomaDB 5747; NeoMap 2008 & 2004	14,191	5,760 ± 200; 17,300 ± 800 yr BP	*Oreamnos harringtoni* dung	Harington and Euler, 1984; Martin, 1984; Mead and Agenbroad, 1989, 1992

TABLE 1—Continued.

Key	Locality name	Database reference	Mean age (cal yr BP)	Cited age	Dating method	References
66	Sudden Shelter	NeoMap 2225; NeotomaDB 5856; 45SV6	7,458	6,310 ± 240; 7,090 ± 85 yr BP	Charcoal	Lucias and Colville, 1980
67	Texas Creek Overlook	NeoMap 1148; NeotomaDB 5197; 5RB2435	458	430 ± 50 yr BP	Charcoal	Creasman and Scott, 1987
68	Upper Sand Island Site	—	12,000	13,000–11,000 cal yr BP	Carving styles	Malotki and Wallace, 2011
69	Walnut Canyon[a]	—	750	1150–1220 AD (Pueblo III)	Ceramics	Starkovich, 2011
70	Walton Creek[a]	NeotomaDB 5202; 5RT11	1,672	1,730 ± 225 yr BP	Charcoal ^{14}C	O'Neil, 1980
71	Wetherill Mesa	NeoMap 1282; NeotomaDB 5316; Site 1644	1,237	1,237 ± 34 cal yr BP	Building foundation style	Hayes and Lancaster, 1975
72	Whiskey Creek	NeoMap 2438; NeotomaDB 5968; LA 4986	1,540	600 ± 32; 2,310 ± 50 cal yr BP (Pueblo III – Early Basketmaker II)	—	Heller, 1976
73	Wither's Wallow	GLCA Accession 82; NAU QSP Site 883	13,900	12,010 ± 160 yr BP	*Mammuthus* dung	Mead and Agenbroad, 1989, 1992
74	Zion	ZION 12396	14,000	Rancholabrean	Pleistocene gravels	Smith and Santucci, 2001; J. Hall, Zion NPS, pers. comm. 2013.

[a] Taxonomic reclassification from *Bos taurus* to *Bison bison*.
[b] Taxonomic classification from "Unknown" to *Bison* sp.
[c] Taxonomic reclassification from *Equus* sp. to *Bison* sp.

Each *Bison* locality on the CP is listed in Table 1 and is numbered consecutively to correspond with the location shown in Figure 1. Undocumented and misidentified specimens from archaeological and paleontological localities are critical to our assessment. These specimens are archived in collections at the Museum of Northern Arizona (MNA), at the Grand Canyon NP, and at the East Tennessee State University Vertebrate Paleontology lab. The previously undescribed specimens consist predominately of dung and skeletal remains from cave, rock shelter, and packrat midden localities. We verified theidentification of each specimen and, if necessary, corrected it using Balkwill and Cumbaa (1992), who improved upon identification guides by Lawrence (1951) and Olsen (1960). In an attempt to capture the full extent of variation, Balkwill and Cumbaa (1992) included every postcranial element and provide 192 quantifiable, osteological characters for comparing *Bison*, represented by 27 individuals of *B. bison bison* and *B. bison athabascae,* and *Bos taurus*, represented by 16 individuals of several breeds including Holstein, Ayrshire, Shorthorn, Longhorn, and Africander. Balkwill and Cumbaa (1992) described specimens of both sexes and of various ages to account for natural variation within *Bison* and *Bos*.

Occurrences of *Bison* were also recovered from the following online data sets: Neotoma Paleoecology Database (NeotomaDB, www.neotomadb.org); Arizona's Cultural Resource Inventory (AZSite, www.azsite.asurite.ad.asu.edu/azsite/); and Neogene Mammal Mapping Portal (NeoMap, www.ucmp.berkely.edu/neomap/). Several localities were in the legal format of Township and Range, which creates a large polygon instead of a point and is imprecise when using point data for other site localities. For each site that was in the legal format, we converted the data into the coordinate system by using a centralized datum in the Township and Range overlay (B. Clark, Earth Point: Township and Range—Public Land Survey System on Google Earth, www.earthpoint.us.; Earth Point Corporation, Kuna, Idaho) in Google Earth Pro (Google Earth Pro, version 7.1.5.1557; Google Inc., Googleplex, Mountain View, California) using decimal degrees. The location is less accurate but more precise for geospatial assessment and analysis.

Each locality has a name and numbering system used by the archiving institution and maintained here. As part of this research, we directly radiocarbon dated *Bison* specimens from two sites, B:16:0461 and Grand Falls. For other sites, the age is

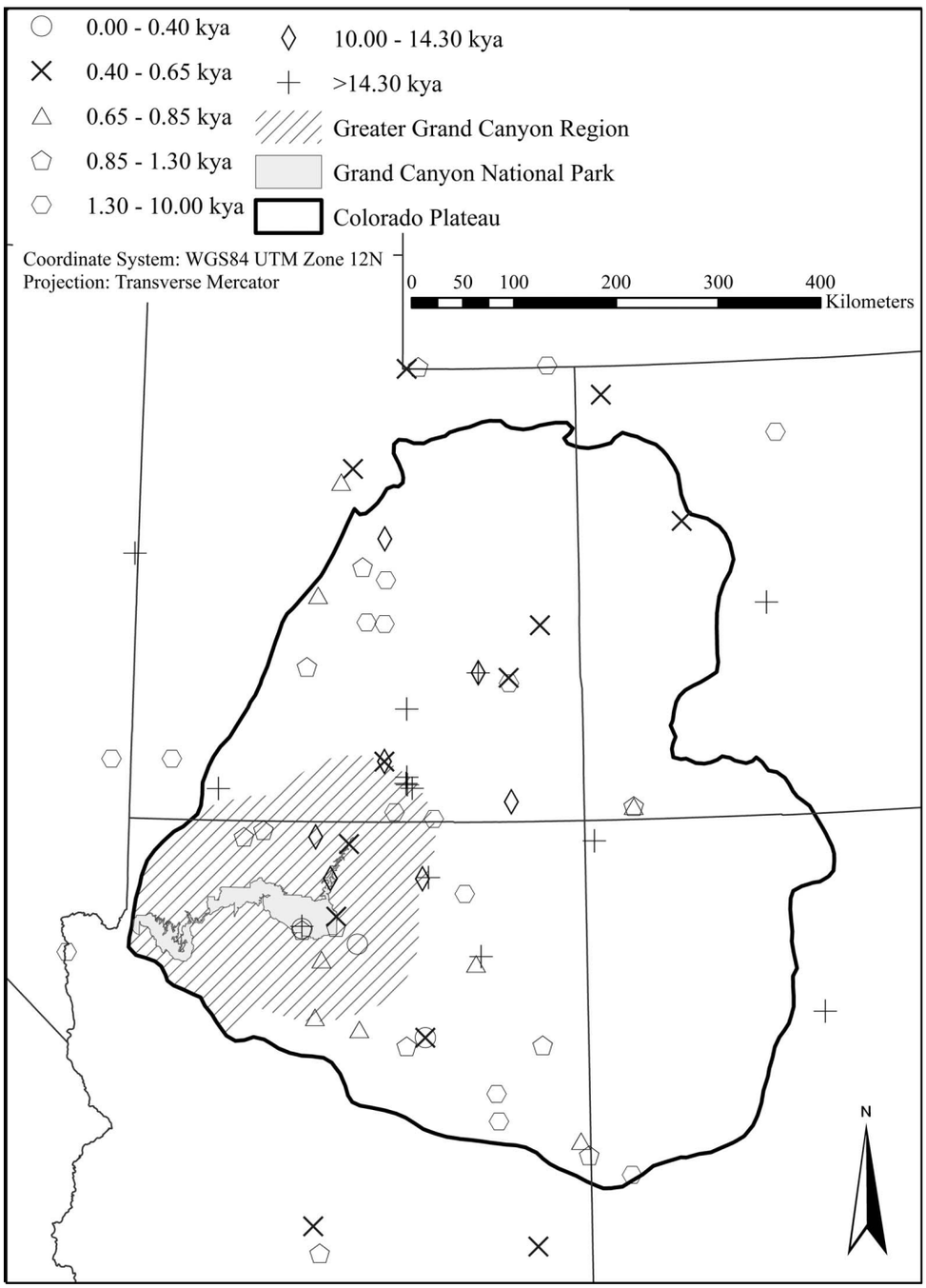

FIG. 2—Map of *Bison* localities placed in chronological context on the Colorado Plateau (CP, heavy black line) and surrounding region. Hashed line represents our definition of the Greater Grand Canyon Region (GGC; see text). Time unit is in thousands of calendar years ago BP (kya).

first given as reported in the literature (if provided) or archival database. We converted the given age(s) to calendar years BP as a single mean geologic age for geospatial representation (Fig. 2). The calibration of the radiocarbon years was completed using OxCal Online Tool (https://c14.arch.ox.ac.uk/) by employing the IntCal13 curve (Reimer et al., 2013). We assumed the average date of the calibrated age to be accurate, but it should be understood to be imprecise. We provide details including pertinent published references, archival databases, and dating sources for each site when available.

North American Quaternary Chronologies—There are a number of chronologies that are defined by specific metrics and cannot be easily integrated because of the inherent differences of paleontological and archaeological definitions; we define these below (Fig. 3). Each chronology used here is necessary for relating our various paleozoological sites that

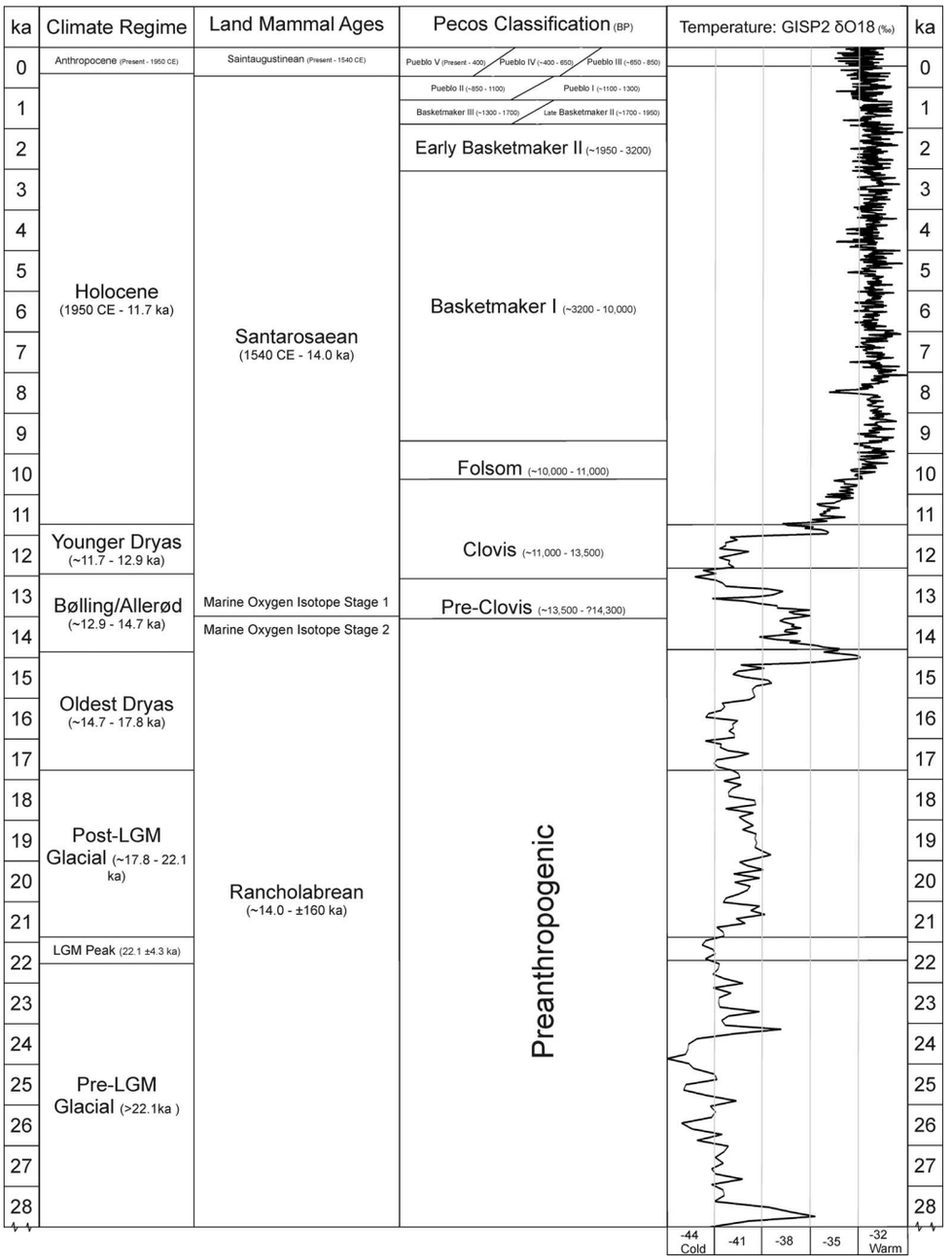

Fig. 3—Integrated North American Quaternary chronology. This time scale displays geological, paleontological (North American Land Mammal Ages: [Bell et al., 2004; Barnosky et al., 2014]), climatic (Climate Regime: Zhao et al., [2005]; Cohen et al., [2013]), and cultural (Pecos Classification: Polyak and Asmerom [2001]) units that are all important for relating *Bison* localities. Not all units are displayed to scale; some cultural units are enlarged for legibility. The relative temperature (solid line) is represented as a proxy derived from δ18-Oxygen isotopes from the Greenland Ice Sheet Project (GISP2). Data from Marine Oxygen Isotope Stages (Anderson et al., 2000); and temperature from GISP2 (Grootes et al., 1993). Abbreviations: ka = kilo annum (thousand years ago); BP, Before Present; CE, Common Era; ‰, part per thousand.

contain *Bison* remains. Furthermore, we implemented a climatic representation for understanding the environmental context of each period.

The Pleistocene is divided into biochronological units referred to as North American Land Mammal Ages based on faunal assemblage components. The Rancholabrean Land Mammal Age is defined by the first appearance of *Bison* south of 55°N latitude and begins approximately 160,000 years BP (Bell et al., 2004). Furthermore, the Rancholabrean Land Mammal Age terminates 14,000 years BP when the Santarosaean Land Mammal Age begins (see discussion in Barnosky et al., 2014, for Land Mammal Age divisions within the Holocene).

Table 2—Temporal summary of *Bison* localities on the Colorado Plateau. "BP" is calendar years Before Present.

Years BP	Pecos classification	Geologic time	*Bison* localities (*n*)
160,000–14,300	Preanthropogenic	Late Pleistocene	14
14,300–10,000	PaleoIndian	Latest Pleistocene	8
10,000–1,300	Archaic	Early to late Holocene	15
1,300–850	Pueblo I–II	Latest Holocene	14
850–650	Pueblo II	Latest Holocene	8
650–400	Pueblo IV	Latest Holocene	12
400–Present	Pueblo V	Latest Holocene	3

In addition to the mammal ages, archaeological stages were implemented based on North American human cultures in the Southwest (Polyak and Asmerom, 2001). The Pecos Classification was used in this study because it is culturally specific to the CP region and to the Southwest, and it often relates to the specimens we observed in museum collections. The later subdivisions of the Pecos Classification are within modern times. For this study, 850 years BP to today, which includes the formal historic, prehistoric, and protohistoric periods, is considered modern times to illustrate *Bison* nativity both precontact and postcontact with Europeans in the Southwest.

Results—Herein, we report 74 sites located on or near the CP (with a few on the periphery) that contain *Bison*. We add 26 localities to the 48 reported in a recent study by Huffer (2013). Moreover, the previous study found that only 16 localities were described from the Holocene, of which 10 were on the CP (Huffer, 2013). In contrast to the Huffer (2013) study, we found 52 sites from the Holocene, of which 40 were on the CP.

Our assessment resulted in the summary data presented in Table 2. We present two sites of interest in and near Grand Canyon NP—B:16:0461 (specimen GRCA 69396) and Grand Falls (specimen MNA V8301; Table 1). We selected these specimens because they were previously insufficiently identified and only relatively dated.

Site B:16:0461, in the Mather Campground area of Grand Canyon NP, was a surface collection that had not been previously reported or identified. It is a lateral half of a proximal phalanx that is identified as *Bison* sp. because the lateral margin is curved (see Balkwill and Cumbaa (1992) and Martin (2014) for discussion). This sample returned a radiocarbon date (Beta 374436) of 50 ± 30 years BP (measured radiocarbon age of 100.5 ± 0.4 pMC).

The Grand Falls specimens represent two nearly complete postcranial individuals deposited 15 m apart in the same arroyo. In collections, these specimens' elements are mostly joined together with consolidant and adhesive. Here, we only describe the right astragalus because it was not treated with consolidant or adhesive. The medial tubercle of the astragalus is on a level with or above the line drawn across the proximal margin of the distal trochlea, as elaborated in Balkwill and Cumbaa (1992). The posterior surface of the astragalus is excavated and extends as far as the lateral margin. Grand Falls was described in the MNA computer database as an arroyo site near the Little Colorado River, which suggests that it is possibly of Pleistocene age. However, radiocarbon dating (Beta 374435) returned an age of 50 ± 30 years BP (measured radiocarbon age of 102.4 ± 0.4 pMC). Subsequently, we placed both B:16:0461 and Grand Falls at the beginning of the 20th century (Pueblo V).

Discussion—Much of what we know about bison on the CP is based on historical and modern studies. Although these are valuable resources, they are incomplete and do not explore the prehistoric record. We found that 13 of our newly identified 26 *Bison* localities (50%) were either previously not identified as *Bison* or were incorrectly identified as "unknown," "large mammal," or "*Bos*." Previous studies rarely identified *Bison* remains from in situ, pre-European contact because it was traditionally thought that *Bison* did not inhabit the CP. We are particularly intrigued that some researchers identified an in situ, pre-European contact faunal remain as "*Bos taurus*," knowing that this taxon arrived with the exploration of Spanish conquistadors, approximately 1540 Common Era. We hope to dispel this persistent line of circular reasoning by providing a thorough assessment of *Bison* on the CP since the latest Pleistocene.

Some hypothesize that the bison found in the Greater Grand Canyon Region were carrion from scavengers, bloat-and-float from upstream Colorado River, or goods traded by peoples. However, it would seem that the pre-Colombian cultural trading of *Bison* elements might not have been traded long distances but more locally (Cannon, 2001). Reed (1952, 1955) points out that the bison skeletal and artifactual remains found in a pre-Spanish context across the southern CP (Arizona) are likely due to trade connections; albeit, Reed does state that the record of bison ("cibola") provided by the Havasupai Indians in the Grand Canyon probably represents a local procurement and not a trade item (independently described in Garcés and Coues, 1900:403, 406).

In addition, *Bison* are not known to frequent caves and are categorized as low frequenters of such shelters, with no more than 16.9% of all *Bison* remains found in caves across the contiguous United States (Jass and George,

2010). Thus, finding *Bison* remains in caves or rock shelters at 45 of 74 (60.8%) sites on the CP appears to be significant because either they were inhabiting the area or they were scavenged from a nearby location. For comparison, approximately 85.7% of bighorn sheep (*Ovis canadensis*) remains are found in caves (Jass and George, 2010).

Conclusion—The direct impact of this study is the production of the first comprehensive review of late Pleistocene and Holocene *Bison* on the Colorado Plateau. The results indicate that the geographic range of fossil and modern *Bison* can be extended to include the CP. Our data imply that *Bison* have been part of the CP from at least approximately 44,000 radiocarbon years ago though the latest Pleistocene (Rancholabrean) to the onset of the Holocene (~11,000 years ago). The past approximately 11,700 years is a critical time because it marks the beginning of the modern climate based on paleobotanical records (McClaran and Van Devender, 1995; Coats et al., 2008). Major ecological and faunal turnover occurred at or by approximately 11,700 years ago, yet the early Holocene climate was still colder than today. The fossil *Bison* record for the early Holocene is not well-reported on the CP, but there appears to be good evidence of *Bison* presence during the late Holocene, through the various cultural phases, and up to the time of European contact. The southern CP (south of the Grand Canyon) in Arizona appears to have been fairly devoid of bison; but, within the Grand Canyon (likely just north of the Colorado River) and north, *Bison* were likely present, albeit never likely abundant based on its record. Though *Bison* were not overly common, such as observed on the Plains, the fossil record clearly demonstrates that this iconic bovid played a role in the biotic communities over much, if not all, of the Colorado Plateau up to the time of European contact.

We thank S. L. Swift and M. Carpenter for the countless hours contributed to data collection and improvement of this project. We thank the National Park Service (ZION 12396, Zion National Park Museum Collection) for the courtesy of abundant information and a specimen approved for destructive radiocarbon analysis (GRCA 69396) from the Grand Canyon National Park (research permit # GRCA-2013-SCI-0052), and C. Hyde and B. Holton for informative discussions about the House Rock Valley bison herd. We thank the Navajo Nation, who in conjunction with the Museum of Northern Arizona provided their specimen for destructive radiocarbon analysis MNA V8301, Loc. 1104 (Navajo Nation Minerals Department research permit date: 30 August 2013). We thank many staff members of the Museum of Northern Arizona for their assistance. S. Emslie and M. Stiger provided important information for bison presence in the Gunnison Basin. We thank the National Buffalo Foundation, the Dr. Ken Throlson American Buffalo Scholarship, Experiment.com (a crowd-sourcing platform), the Western Bison Association, the East Tennessee State University (ETSU) Don Sundquist Center of Excellence in Paleontology, and the ETSU Graduate School Graduate Student Research Grant for providing funds to JMM. We appreciate the continued support of The Mammoth Site and contribution of anonymous reviewers for much improvement of the manuscript.

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Submitted 7 July 2016. Accepted 19 December 2016.
Associate Editor was Troy Ladine.

Queries for swna-62-01-03

This manuscript/text has been typeset from the submitted material. Please check this proof carefully to make sure there have been no font conversion errors or inadvertent formatting errors. Allen Press.