



A fossil *Bison antiquus* from Puebla, Mexico and a new minimum age for the Valsequillo fossil area

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ABSTRACT

The genus *Bison* originated in Indochina, and was mainly a Holarctic taxon, known from the North America, initially with *Bison latifrons* from the early Rancholabrean, and several other species, including the recent one *B. bison*. Here a new record of *Bison antiquus* based on several calvaria and horn cores from Valsequillo Basin, Puebla, Mexico is documented. Based on taxonomic characters we identify two morphologies of *B. antiquus* among the studied fossils: the "antiquus" morphology and the "occidentalis" morphology. A radiocarbon age of 7151 ± 70 years BP obtained from a calvarium of *B. antiquus* with "antiquus" morphology, representing the youngest record in North America for this morphology, as well as the first evidence of an early Holocene record for the species in Mexico.

1. Introduction

The genus *Bison* originated in Indochina during the Villafranchian, between the Late Pliocene and Early Pleistocene (Kurtén, 1968; McDonald, 1981; Martínez-Navarro et al., 2007, 2011; Khan et al., 2010; Castaños et al., 2012). It fastly spread through temperate Eurasia, reaching the Iberian Peninsula between 3.4 and 2.6 million years ago (Ma) (Vekua, 1995; Cuenca-Bescós and García, 2007; Lordkipanidze et al., 2007; Pavia et al., 2012; Masini et al., 2013; Van der Made, 2013; Palombo, 2016). Afterward, during the Middle Pleistocene, *B. schoetensacki* evolved in Europe, and *B. priscus* evolved and extended from Boreal Eurasia into Beringia between 195,000 and 135,000 years BP (Skinner and Kaisen, 1947; Kurtén, 1968; McDonald, 1981; Shapiro et al., 2004; Vercoutère and Guérin, 2010; Palacio et al., 2017). From there, and during the Sangamonian, *Bison* entered continental North America below 55° of latitude, and produced the first autochthonous species, *Bison latifrons*, dated at 160,000 years BP (McDonald, 1981;

Haynes, 1985; Bell et al., 2004; Shapiro et al., 2004; Froese et al., 2017). The second wave of invasion, during the Wisconsinan, dated approximately 50,000 years BP, produced the second autochthonous species, *Bison antiquus*, which was the most common in North America, spreading across Mexico, reaching as far as Nicaragua (McDonald, 1981). Also, during this time, *B. priscus* entered North America along with another allochthonous species, *B. alaskensis*, with the latter reaching as far as the Basin of Mexico (Hibbard and Villa-Ramírez, 1950; Hibbard, 1955; McDonald, 1981; Haynes, 1985; Bell et al., 2004; Shapiro et al., 2004).

Finally, there are five recognized *Bison* species for the Quaternary of Mexico: *B. alaskensis*, *B. antiquus*, *B. latifrons*, and *B. priscus* from the Late Pleistocene (Cope, 1884; Villada, 1903; Osborn, 1905; Skinner and Kaisen, 1947; Hibbard and Villa-Ramírez, 1950; De Terra, 1953; Hibbard, 1955; Downs, 1956; Cracraft, 1968; Mooser and Dalquest, 1975; Ferrusquía-Villafranca and Torres-Roldán, 1980; McDonald, 1981; Álvarez, 1982; Carranza-Castañeda and Miller, 1987; Franzen, 1993,

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1994; Pichardo, 1997, 1999; Solorzano, 2002; Lucas, 2008a, 2008b; Jiménez-Hidalgo et al., 2013; Díaz-Sibaja et al., 2018; Sánchez Salinas et al., 2016), and *B. bison* from the Holocene, which arose from *B. antiquus* between 4000 and 5000 years BP in southern Canada via a transitional form sometimes referred as *B. "occidentalis"* (syn. *B. antiquus*) (McDonald and Lammers, 2002; Wilson et al., 2008; Díaz-Sibaja et al., 2018).

Bison occidentalis was described by Lucas in 1898 from a partial skull from Fort Yukon, Alaska. It was regarded as a separate species from *B. antiquus* by several authors (e.g. Lucas, 1899; Skinner and Kaisen,

1947), and also as a synonym of *B. bison* (e.g. Kurtén and Anderson, 1980). However, McDonald (1981) considered it as a subspecies of *B. antiquus*, and a transitional form to *B. bison*. This hypothesis is partially supported by molecular data, which points out to a transition from *B. antiquus* to *B. bison*, through *B. antiquus* with the "occidentalis" morphology between 4 and 5 Ka BP in southern Canada, nevertheless *B. a. antiquus* and *B. a. occidentalis* are not retrieved as monophyletic (Shapiro et al., 2004; Wilson et al., 2008). Also, "*Bison occidentalis*" is shown to be a chronospecies with smaller body size than the older *Bison antiquus*, a condition linked to the increase in global temperatures

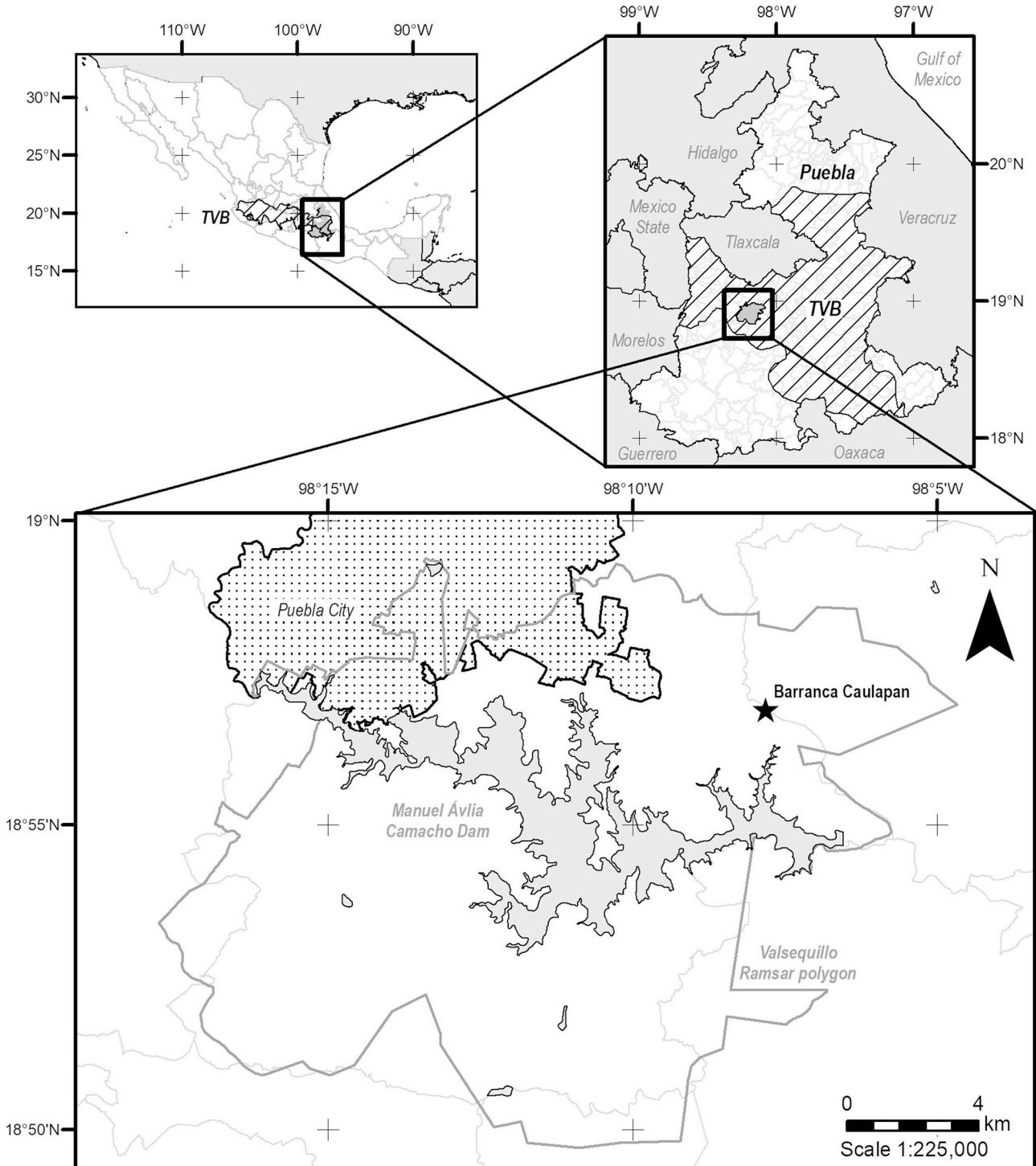


Fig. 1. Location map of the Barranca Caulapan locality, at Valsequillo Basin, Puebla, Mexico. TVB, Trans-Mexican Volcanic Belt.

between 20 and 5 Ka BP (Martin et al., 2018). Thus, we do not consider *Bison antiquus occidentalis* and *B. a. antiquus* as valid subspecies, and rather a single species: *Bison antiquus*, with two morphologies, termed here as “antiquus” and “occidentalis” in which the later was an evolutionary grade, heavily influenced by climate change.

Some authors propose that *Bison antiquus* (including *B. antiquus occidentalis*) can be synonymized with *Bison bison* and consider them as subspecies (e.g. Wilson, 1974; Kurtén and Anderson, 1980). Nevertheless, as McDonald (1981) pointed out their horn core morphology and dimensions can distinguish these forms. Even if they form a big ana-genetic line that ends in *B. bison* (Shapiro et al., 2004; Wilson et al., 2008; Froese et al., 2017), their ecological behavior was completely different and is better understood if *B. bison* and *B. antiquus* are considered as separate species (Rivals et al., 2007; Rivals and Semperebon, 2012; Díaz-Sibaja et al., 2018). A position supported on the basis that *B. bison* is monophyletic and had a single origin (Shapiro et al., 2004; Wilson et al., 2008).

In this work, we study a fossil specimen of *Bison* from Valsequillo Basin, Puebla, Mexico, constituting the first record of a Holocene *Bison antiquus* with the “antiquus” morphology, which changes our understanding of the age of this Paleoindian occupation site, as well as the biogeochronological and biogeographic understanding of bison evolution.

2. Materials and methods

2.1. Study area

The fossil area of Valsequillo Basin (Fig. 1) is located in central Mexico, within the Trans-Mexican Volcanic Belt morphotectonic province, in the state of Puebla, southeastern Puebla city (Stevens et al., 2012). It comprises a local fauna (*sensu* Woodburne, 2004) with several Late Pleistocene localities, of which, the most important ones include Arenillas, Atepetzingo, Hueyatenco and Barranca Caulapan (Pichardo, 1997; Metcalfe et al., 2016). Barranca Caulapan is usually divided into two discrete localities, Upper Caulapan (actually named Barranca Coahuilapa) and Lower Caulapan, separated only by a distance of 700 m (INEGI, 2010; Stevens et al., 2012). The fossil material of this study comes from the Valsequillo Basin, but the exact provenance is unknown. Only the specimen CRINAHP-0521 has a specific locality and come from the “Lower” Barranca Caulapan (18°56.897'N, 98° 07.812'W), and not from Barranca Coahuilapa.

2.2. Stratigraphy

The Valsequillo Quaternary deposits overlay Cretaceous rocks of the Balsas group. The Pleistocene sediments comprises 70–100 m in four major units: the Amomoloc lake beds (also termed Lower Lake beds), the Xalnene tuff, the Atoyatenco lake beds (also named Upper Lake beds, which contained the Batan Lahar, sometimes referred as a distinctive unit), and the Valsequillo gravels at the top (Stevens et al., 2012; Metcalfe et al., 2016). The Valsequillo gravels unit is distributed near the Manuel Ávila Camacho Dam (also known as Valsequillo reservoir, a Ramsar site), and in the Barranca Caulapan and Barranca Coahuilapa sites (Metcalfe et al., 2016). The sequence of Barranca Caulapan comprises intercalated gravels from 16 up to ~100 mm in diameter alternated with massive undifferentiated sands and silts (Szabo et al., 1969; Stevens et al., 2012).

2.3. Radiometric dating

A sample of 2 g of bone from the trabeculae at the frontal sinus of calvarium CRINAHP-1648 was collected. The sample was processed at the Laboratorio de Espectrometría de Masas con Aceleradores (LEMA-FPS05-01) at Universidad Nacional Autónoma de México (UNAM).

The sample was cleaned using deionized water (10–18 MΩ cm). Once

dry it was pulverized and later treated using a chemical procedure with HCl (0.5 M) at low temperature, for dissolving the mineral phase and removing the carbonates. Gelatinization was then carried out by means of acid treatment with HCl (0.2 M) at high temperatures. The dissolved collagen was filtered to preserve the fibers greater than 30 KD, thus obtaining the ultrafiltered collagen. The carbon sampled obtained was converted to CO₂ and later in pure graphite, using an Automated Graphitization Equipment (AGEIII) of Ion Plus. A¹⁴C, ¹³C and ¹²C analysis from graphite were carried out with an accelerator spectrometry of mass. From the obtained values, the Radiocarbon Age (¹⁴C) was calculated, given in years before of present. The Radiocarbon Age was corrected by δ¹³C fractionation from the ratio of ¹³C/¹²C in the sample. The software package for the calibration of radiocarbon dates 96 OxCal/ORAU with the InCal13 curve (Ramsey and Lee, 2013) was employed. Two types of calibrated ages were obtained: age calibrated before present (calBP), and calendar age before Christ (calBC). For each one the most probably intervals were calculated, with a confidence level of 68% (1σ) and 95% (2σ) (Fig. 2).

2.3.1. Nomenclatural acts

In this work, we follow the anatomical terminology and sex identification proposal by McDonald (1981). For the measurements, we follow Skinner and Kaisen (1947) and McDonald (1981).

2.3.2. Repositories and institutional abbreviations

The specimens figured and examined in this study are deposited on the following institutions: Centro INAH-Puebla (Instituto Nacional de

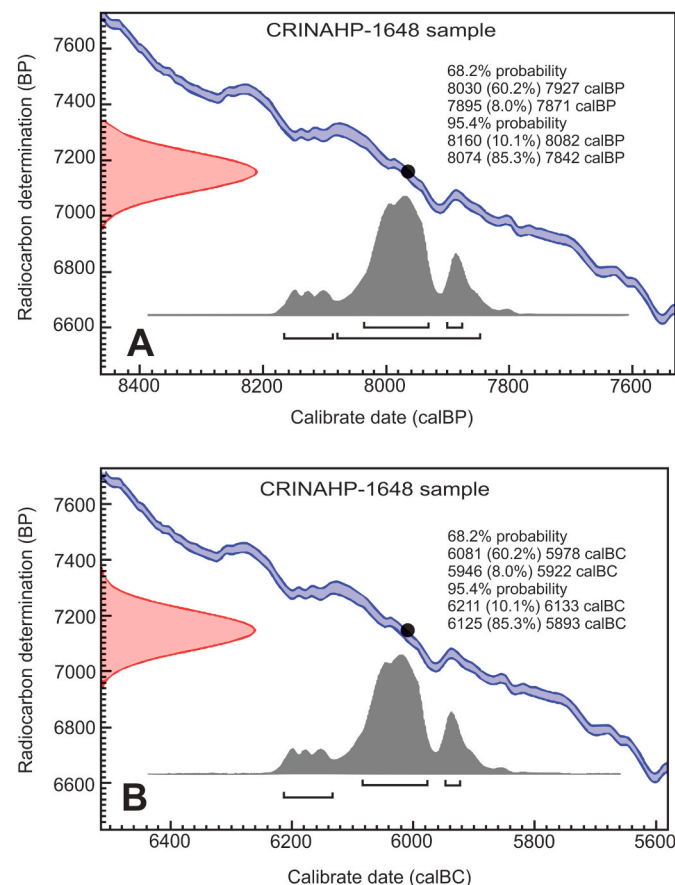


Fig. 2. Graph that shows the determination of Carbon date for the sample calibration with confidence intervals. The black dot is the interpolation point into the calibration curve (blue curve). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Antropología e Historia, Puebla) under the acronym CRINAHP, and the Laboratorio de Arqueozoología “M. en C. Ticul Álvarez Solórzano”, Subdirección de Laboratorios y Apoyo Académico del Instituto Nacional de Antropología e Historia (INAH).

3. Systematic paleontology

Order Ruminantia [Scopoli, 1777](#).

Family Bovidae [Gray, 1821](#).

Genus *Bison* ([Hamilton-Smith, 1827](#)).

Species *Bison antiquus* [Leidy \(1852\)](#).

[Figs. 3.1 to 3.7](#).

3.1. Diagnosis

For the horn cores: posterior margin straight, longitudinal axis arched, growth straight along the longitudinal axis, base symmetrical (in cross-section: isosceles for males, circular to elliptical for females), distal tip slightly curved upwards, length along upper curve between >175 and < 400 mm ([McDonald, 1981](#)).

3.2. Materials

CRINAHP-0521, one isolated horn core, with partial frontal bone preserved, and complete burr; CRINAHP-0884, isolated horn core, broken at the burr; CRINAHP-1648, one calvarium, preserving the occipital and frontal regions, with both horn cores; CRINAHP-1790, isolated horn core, broken at the burr; CRINAHP-2302, one calvarium, preserving the occipital and frontal regions, with both horn cores; CRINAHP-2303, one calvarium, with the occipital region, the frontal region only at the beginning of the orbits with both horn cores; INAH 66-R-14-16, one calvarium with occipital and frontal regions preserved, only with the right horn core.

3.3. Description

CRINAHP-1648, CRINAHP-2302, CRINAHP-2303, and INAH 66-R-14-16 are calvaria with both horn core bases, only INAH 66-R-14-16 lacks the left horn core. All of these have the usual *Bison* morphology: the horn core bases emerging at right angle with respect to the longitudinal skull axis, those bases do not rise from the plane of the frontals, which are wide and flattened; the posterior occipital region is robust and have robust and wide occipital condyles; finally the margin of the orbits, present in CRINAHP-2302, CRINAHP-2303, and INAH 66-R-14-16, show a tube-like orbit ([Lucas, 1899](#); [Skinner and Kaisen, 1947](#); [McDonald, 1981](#)). All of these morphological characters excludes the possibility that some of these calvaria belong to the genus *Bos*, as traditionally defined.

The horn cores present in the calvaria also display a typical *Bison* morphology: large, robust, and are not curved anteriorly ([McDonald, 1981](#)). Also, these specimens along with the isolated horn cores (CRINAHP-0884, CRINAHP-1790, and CRINAHP-0521) show a typical *Bison antiquus* morphology: a symmetrical horn core base about dorso-ventral axis, the posterior margin is straight, the growth, as well as the striae on the surface of the horns are straight along an arched longitudinal axis ([McDonald, 1981](#)). This morphology differs from *Bison priscus* and *B. alaskensis*, other recognized Late Pleistocene to Early Holocene *Bison* species in North America. *Bison priscus* and *B. alaskensis* have horn cores with asymmetrical bases (isosceles in cross-section), with a sinuous posterior margin, and the growth as well as the striae along the horn core longitudinal axis are spiraled ([McDonald, 1981](#)). The antero-posterior margin of the horn cores present in the calvaria are nearly parallel with the frontal plane, while in *B. priscus* and *B. alaskensis*, this plane is rotated forward with respect of the frontal plane ([McDonald, 1981](#)). All of these leads us to assign the Valsequillo fossil bison of this study to *B. antiquus*.

4. Results

We analyzed four calvaria and three isolated horn cores. The calvaria CRINAHP-1648 ([Fig. 3.1](#)), CRINAHP-2302 ([Fig. 3.2](#)), CRINAHP-2303 ([Fig. 3.3](#)), and INAH 66-R-14-16 ([Fig. 3.7](#)) belonged to adult males. Only one horn core, CRINAHP-0884, belonged to a female ([Fig. 3.4](#)), while CRINAHP-1790 ([Fig. 3.5](#)), and CRINAHP-0521 ([Fig. 3.6](#)) were males ([McDonald, 1981](#)).

We found two morphologies in *Bison* specimens examined (antiquus and occidentalis), although they belong to the same species, *Bison antiquus*. CRINAHP-1648, CRINAHP-2302, and CRINAHP-2303 calvaria, as well as CRINAHP-0884, and CRINAHP-1790 horn cores belong to the “antiquus” morphology. While the INAH 66-R-14-16 calvarium and the CRINAHP-0521 horn core were assigned to the “occidentalis” morphology ([McDonald, 1981](#); [Frison, 1998](#)). A morphometric summary of these calvaria, as well as literature with means of both morphologies (i.e. “antiquus” and “occidentalis”) are presented in [Table 1](#).

A radiocarbon age of 7151 ± 70 years BP for CRINAHP-1648 calvarium was obtained. This age places this specimen at the Middle Holocene, within the Northgrippian Stage, and within the Santarosean North American Land Mammal Age (NALMA) ([Barnosky et al., 2014](#)). We were not able to date other specimens on this study since we were unable to obtain collagen from them.

5. Discussion

5.1. The *Bison* of Valsequillo

The *Bison antiquus* morphologies (i.e. antiquus and occidentalis) can be distinguished based on morphology ([McDonald, 1981](#); [Frison, 1998](#)). The specimens INAH66-R-14-16 and CRINAHP-0521 were assigned to the “occidentalis” morphology due to their characteristics, which includes smaller, slender, posteriorly directed horn cores, with a curved tip which has a circular to elliptical cross-section, with a posterior margin straight or slightly concave, and with a reduction or total lack of the dorsal groove ([Lucas, 1899](#); [Skinner and Kaisen, 1947](#); [McDonald, 1981](#)). The rest of the fossil remains in this study were assigned to the “antiquus” morphology, which consists in larger horn cores, directed at approximately 90° from the middle line of the frontals, the tip is triangular to cordiform in cross-section, their posterior margin is straight, and have a well-developed dorsal groove ([McDonald, 1981](#)).

It is noticeable that the INAH 66-R-14-16 has a non-traditional morphology among the “occidentalis” morphology, with horn cores placed high above the frontals, resembling those of the northern *B. priscus* ([Skinner and Kaisen, 1947](#)), a species previously reported at Valsequillo Basin ([Guenther, 1968](#); [Pichardo, 1997](#)). Nevertheless, the horn core INAH 66-R-14-16 lacks the morphology of *B. priscus*, which includes an asymmetrical base, posterior margin sinuous, and a spiraled growth axis ([McDonald, 1981](#)). Thus, all the *Bison* remains from Valsequillo Basin studied in this work belong to *B. antiquus*.

The differences observed between these fossil remains are in accordance with the morphological variation of *Bison antiquus* occurring in the same deposits (e.g. [Wilson et al., 2008](#)). Also, this supports the idea that “*Bison antiquus occidentalis*” is not a valid species or subspecies, and rather, a transitional ecotype, leading to *Bison* ([McDonald and Lammers, 2002](#); [Shapiro et al., 2004](#); [Wilson et al., 2008](#)).

Another possibility is that fossil Valsequillo bison in this study might belong to different stratigraphic levels, with differences in the climate, thus producing the observed morphological patterns. This is supported not only by the morphological adaptability of *Bison antiquus* ([Martin et al., 2018](#)), but also by the adaptability and morphological disparity observed in the modern *Bison*. This species was previously believed to have two different subspecies: *B. b. bison*, the plains bison, and *B. b. athabascae*, the wood bison (e.g. [Van Zyll de Jong, 1986](#); [McDonald, 1981](#)). These were shown to have different ecological behaviors



Fig. 3. Cranial elements of *Bison antiquus* from Valsequillo Basin, Puebla, Mexico. *Bison antiquus* “antiquus” morphology: (1) CRINAHP-1648, (2) CRINHAP-2302, and (3) CRINHAP-2303, calvaria with both horn cores; (4) CRINAHP-0884 and (5) CRINAHP-1790, isolated horn cores. *Bison antiquus* “occidentalis” morphology: (6) CRINAHP-0521 isolated horn core; (7) INAH 66-R-14-16, calvarium with the right horn core. Scale bar = 10 cm.

Table 1

Bison antiquus calvaria morphometry summary. (1) Spread of horn cores, tip to tip; (2) Horn core length, upper curve, tip to burr; (3) Straight line distance, tip to burr, dorsal horn core; (4) Minimum circumference, horn-core base. *B. antiquus* “antiquus” (N [1] = 77, N [2] = 86, N [3] = 81, N [4] = 89) and “occidentalis” (N [1] = 27, N [2] = 32, N [3] = 30, N [4] = 38) measurements from McDonald (1981). All measurements in millimeters.

Collection number	1	2	3	4
CRINAHP-1648	858	323	266	315
CRINAHP-2277	869	268	198	296
CRINAHP-2276	686	301	209	317
INAH 66-R-14-16	–	265	207	252
CRINAHP-0884	–	210	220	–
CRINAHP-1790	–	325	250	285
CRINAHP-0521	–	275	214	297
<i>B. antiquus</i> “antiquus” (males)	870 ± 13.7	279.2 ± 6.2	249.7 ± 5.3	324.4 ± 5.3
<i>B. antiquus</i> “antiquus” (females)	669.5 ± 15.9	202.9 ± 5.1	190.1 ± 5	209 ± 3.3
<i>B. antiquus</i> “occidentalis” (males)	779.3 ± 8.8	277.8 ± 4.2	248.1 ± 3.5	300.3 ± 2.9
<i>B. antiquus</i> “occidentalis” (females)	614.4 ± 14.2	197.1 ± 4.4	182.9 ± 3.5	191.5 ± 2.7
<i>Bison</i> (males)	603.9 ± 3.9	190.7 ± 2.1	172.4 ± 1.9	255.4 ± 1.6
<i>Bison</i> (females)	451 ± 6.6	124.1 ± 3	171.1 ± 2.7	162.1 ± 1.9

(Guthrie, 1990). Nevertheless, the subspecies status of the wood bison was challenged, and it was suggested it was merely an ecomorph (Geist, 1991). This idea was further explored with genetic data, leading to the conclusion that the modern wood bison represent a locally adapted variety of *B. bison* that had interbreed with the few remaining ancient wood bison, and thus, was not a valid subspecies (Groves and Grubb, 2011). If this is the case with Valsequillo’s fossil bison, remains should be further explored with more detailed stratigraphic works and paleoecological inferences, such as stable isotopes and dental wear.

5.2. The age of *Bison antiquus* and the Valsequillo fossil site

There are several dubious ages attributed to *B. antiquus*, with no cranial material associated or obtained with non-diagnostic fossil remains (e.g. Nielsen et al., 1984). The youngest of those ages comes from Anchorage, Alaska, with a radiocarbon age of 470 ± 90 years BP for a horn sheath identified ambiguously as *B. antiquus* “occidentalis” (Harrington, 2003).

One of the youngest non-ambiguous records of *B. antiquus* with the “antiquus” morphology comes from Rancho La Brea, with a radiocarbon age of 10,900 ± 240 years BP (Marcus and Berger, 1984). On the other hand, the youngest records of *B. antiquus* with the “occidentalis”

morphology comes from Hughes Bog, Iowa, with a radiocarbon age of 5640 years BP (McDonald, 1981), and from Kenora, Ontario, with a radiocarbon age of 4270 ± 65 years BP (McDonald and Lammers, 2002).

The CRINAHP-1648 calvarium and its radiocarbon age of 7151 ± 70 years BP represent the youngest record for the *B. antiquus* “antiquus” morphology in North America. Also, it suggests that a new minimal radiocarbon age for the megafaunal species in the Valsequillo Basin can be established. As this age is based on one specimen, more studies are required in order to confirm the minimal age of the Valsequillo local fauna.

At Valsequillo Basin, the previously reported minimum age for *B. antiquus* was 9150 ± 500 years BP (McDonald, 1981). Nevertheless, McDonald (1981) assigned this age for both *B. antiquus* morphologies (Tables 24 and 28 in McDonald, 1981). This age was not obtained from bone samples, but from a gastropod radiocarbon sample (W-1898) at the “lower” Barranca Caulapan site (Szabo et al., 1969). Afterward, this age was assigned to the Valsequillo “Faunal zone I”, in association with typical Late Pleistocene megafaunal species, excluding *Bison* and bifacial stone tools (Pichardo, 1997). *Bison* was believed to belong to the “Faunal zone II”, dated at Barranca Caulapan with a radiocarbon age obtained also from snails of 21,850 ± 850 years BP, and the presence of unifacial stone tools (Szabo et al., 1969; Pichardo, 1997, 1999). Nevertheless, we found *Bison antiquus* at the proposed “Faunal zone I”, demonstrating that it is not an index taxon as previously proposed by Pichardo (1997, 1999). Thus, the Barranca Caulapan site has ages ranging from >35,000 (Szabo et al., 1969; Metcalfe et al., 2016) to 7151 (this work) years BP. And until a controlled stratigraphic work is done with the stone tools, there is no certainty of the age of those human-produced elements (see an extensive revision for the datings at Valsequillo at Gonzalez et al., 2017).

6. Conclusions

The fossil bison of the Valsequillo Basin includes only one species, *Bison antiquus*, with two different morphologies: (1) *B. antiquus* “antiquus” and (2) *B. antiquus* “occidentalis”. A calvarium of *B. antiquus* “antiquus” morphology (CRINAHP-1648) was dated at 7151 ± 70 years BP, which is the youngest age for any previously reported *Bison antiquus* from Mexico, and it is the youngest “antiquus” morphology in North America. This age provides a new minimum age for the fossil area of Valsequillo Basin, and raises questions about the ages previously reported for stone tools from this Paleoindian site. Further detailed stratigraphic and radiometric studies are required in this area to clarify the temporal ranges of its extinct fauna and human occupation dates.

The presence of two morphologies of *Bison antiquus* at Valsequillo Basin suggests that other previously recognized species such as *B. priscus* were in fact, *B. antiquus* specimens. This high degree of horncore variation also suggests that a more detailed study of the ages and

stratigraphy of these, and other specimens are required to confirm that the two chronospecies (regarded in this work as *antiquus* and *occidentalis* morphologies) were present at different times in the Valsequillo Basin.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

- Barnosky, A.D., Holmes, M., Kirchholtes, R., Lindsey, E., Maguire, K.C., Poust, A.W., Stegner, M.A., Sunseri, J., Swartz, B., Swift, J., Villavicencio, N.A., Wogan, G.O.U., 2014. Prelude to the anthropocene: two new North American Land mammal ages (NALMAs). *The Anthropocene Review* 1, 225–242. <https://doi.org/10.1177/2053019614547433>.
- Bell, C.J., Lundelius Jr., E.L., Barnosky, A.D., Graham, R.W., Lindsay, E.H., Ruez Jr., D.R., Semken Jr., H.A., Webb, S.D., Zakrzewski, R.J., 2004. The blanford, irvingtonian, and rancholabrean mammal ages. In: Woodburne, M.O. (Ed.), *Late Cretaceous and Cenozoic Mammals of North America. Biostratigraphy and Geochronology*. Columbia University Press, N. Y., pp. 232–314.
- Carranza-Castañeda, O., Miller, W.E., 1987. Rediscovered type specimens and other important published Pleistocene mammalian fossils from central Mexico. *J. Vertebr. Paleontol.* 7 (3), 335–341. <https://doi.org/10.1080/02724634.1987.10011664>.
- Castañes, J., Castaños, P., Murelaga, X., Alonso-Olazabal, A., 2012. Kiputz Ix: un conjunto singular de bisonte estepario (*Bison priscus* Bojanus, 1827) del Pleistoceno Superior de la Península Ibérica. *Ameghiniana* 49, 247–261. [https://doi.org/10.5710/AMGH.v49i2\(529\)](https://doi.org/10.5710/AMGH.v49i2(529)).
- Cope, E.D., 1884. The extinct mammalia of the valley of Mexico. *Proc. Am. Phil. Soc.* 22 (117), 1–21.
- Cracraft, J., 1968. First record of the Turkey *Meleagris gallopavo* from the Pleistocene of Mexico. *Condor* 70 (3), 274. <https://doi.org/10.2307/1366706>.
- Cuenca-Bescós, G., García, N., 2007. Biostratigraphic succession of the early and middle Pleistocene mammal faunas of the atapuerca cave sites (burgos, Spain). *Cour. Forschungsinst. Senckenberg* 259, 99–110.
- De Terra, H., 1953. A strange Pleistocene fossil locality in Mexico. *Science* 118 (3077), 748–749.
- Díaz-Sibaja, R., Jiménez-Hidalgo, E., Ponce-Saavedra, J., García-Zepeda, M.L., 2018. A combined mesowear analysis of Mexican *Bison antiquus* shows a generalist diet with geographical variation. *J. Paleontol.* 92 (6), 1130–1139. <https://doi.org/10.1017/jpa.2018.19>.
- Downs, T., 1956. Fossil vertebrates from lago de Chapala, Jalisco, Mexico. *Congreso Geol. Int.* 75–77.
- Ferrusquía-Villafranca, I., Torres-Roldán, V., 1980. El registro de mamíferos terrestres del Mesozoico y Cenozoico de Baja California. *Universidad Nacional Autónoma de México, Instituto de Geología, Revista*, pp. 56–62.
- Franzen, J.L., 1993. Eine eiszeitliche Säugetierfauna aus Minä, N.L. (Mexiko). *Preparator* 39 (2), 67–72.
- Franzen, J.L., 1994. Eine Rancho-La-Brea-Fauna aus Nordost-Mexiko (Bundesstaat Nuevo León). *Nat. Mus.* 124 (8), 241–258.
- Frison, G.C., 1998. Paleoindian large mammal hunters on the plains of North America. *Proc. Natl. Acad. Sci. U.S.A.* 95, 14576–14583. <https://doi.org/10.1073/pnas.95.24.14576>.
- Froese, D., Stiller, M., Heintzman, P.D., Reyes, A.V., Zazula, G.D., Soares, A.E.R., Meyer, M., Hall, E., Jensen, B.J.L., Arnold, L.J., MacPhee, R.D.E., Shapiro, B., 2017. Fossil and genomic evidence constraints the timing of bison arrival in North America. *Proc. Natl. Acad. Sci. U.S.A.* 114, 3457–3462. <https://doi.org/10.1073/pnas.1620754114>.
- Geist, V., 1991. Phantom Subspecies: the Wood Bison *Bison bison* “*athabascae*” Rhoads 1897 is not a valid taxon, but an ecotype. *Artic* 4, 283–300.
- Gonzalez, S., Huddart, D., Bennett, W., 2017. Valsequillo Pleistocene archaeology and dating: ongoing controversy in Central Mexico. *World Archaeol.* 38, 611–627.
- Groves, C., Grubb, P., 2011. *Ungulate Taxonomy*. The Johns Hopkins University Press, pp. 1–309.
- Gray, J.E., 1821. On the natural arrangement of vertebrate animals. *London Medical Repository. Monthly J. Rev.* 15, 296–310.
- Guenther, E.W., 1968. Untersuchungen zur jungeszeitlichen und nacheiszeitlichen geologischen und paläontologischen Geschichte. *El proyecto México de la Fundación Alemana para la Investigación Científica-Franz Steiner Verlag. GMBH* 1, 32–36.
- Guthrie, R.D., 1990. *Frozen Fauna of the Mammoth Steppe. The Story of Blue Babe*. The University of Chicago Press.
- Hamilton-Smith, C., 1827. Synopsis of the species of the class Mammalia, as arranged with reference to their organization by Cuvier and other naturalists: with specific characters, synonymy. A synopsis of the species of the Class Mammalia. Order VII. Ruminantia. Pecora, Lin. In: Griffith, E. (Ed.), *The Class Mammalia Arranged by the Baron Cuvier, with Specific Descriptions. The Animal Kingdom Arranged in Conformity with its Organization, by the Baron Cuvier, Member of the Institute of France, with Additional Descriptions of All the Species Hiterto*. Geo. B. Whittaker, London, pp. 296–391.
- Harington, C.R., 2003. *Annotated Bibliography of Quaternary Vertebrates of Northern North America: with Radiocarbon Dates*. University of Toronto Press in collaboration with the Canadian Museum of Nature, p. 539.
- Haynes, C.V., 1985. Mastodon-bearing springs and late Quaternary geochronology of the Lower Pomme de Terre Valley, Missouri, vol. 204. *Geological Society of America Special Paper*, pp. 1–35.
- Hibbard, C.W., 1955. Pleistocene Vertebrates from the Upper Becerra (Becerra Superior) Formation, Valley of Tequixquiac, Mexico, with Notes on Other Pleistocene Forms. *Contributions from the Museum of Paleontology*, vol. 12. University of Michigan, pp. 47–96.
- Hibbard, C.W., Villa-Ramírez, B., 1950. El bisonte gigante de México. *Anales del Instituto de Biología* 21, 243–251.
- INEGI, 2010. *Red Hidrográfica Escala 1:50 000 Edición 2.0. Subcuenca RH18Ab - R. Atoyac - Balcón del Diablo*.
- Jiménez-Hidalgo, E., Cabrera-Pérez, L., MacFadden, B.J., Guerrero-Arenas, R., 2013. First record of *Bison antiquus* from the late Pleistocene of southern Mexico. *J. S. Am. Earth Sci.* 42, 83–90. <https://doi.org/10.1016/j.jsames.2012.07.011>.
- Khan, M.A., Kostopoulos, D.S., Akhtar, M., Nazir, M., 2010. *Bison* remains from the upper siwaliks of Pakistan. *Neues Jahrbuch Geol. Palaontol. Abhandl.* 258, 121–128. <https://doi.org/10.1127/0077-7749/2010/0090>.
- Kurtén, B., 1968. *Pleistocene Mammals of Europe*. Weidenfeld & Nicolson, p. 317.
- Kurtén, B., Anderson, E., 1980. *Pleistocene Mammals of North America*. Columbia University Press, p. 442.
- Leidy, J., 1852. *Memoir on the extinct species of American ox*. *Smithsonian Contrib. Knowl.* 5, 3–20.
- Lordkipanidze, D., Jashashvili, T., Vekua, A., Ponce de León, M.S., Zollikofer, C.P.E., Rightmire, G.P., Pontzer, H., Ferring, R., Oms, O., Tappen, M., Bukhsianidze, M., Agusti, J., Kahlke, R., Kiladze, K., Martínez-Navarro, B., Mouskhelishvili, A., Nioradze, M., Rook, L., 2007. Postcranial evidence from early *Homo* from Dmanisi, Georgia. *Nature* 449, 305–310. <https://doi.org/10.1038/nature06134>.
- Lucas, F.A., 1899. The fossil bison of North America. *Proc. U. S. Natl. Mus.* 21, 755–771. <https://doi.org/10.5479/si.00963801.21-1172.755>.
- Lucas, S.G., 2008a. Late Cenozoic fossil mammals from the Chapala rift basin, Jalisco, Mexico. *New Mexico Mus. Nat. Hist. Sci. Bull.* 44, 39–50.
- Lucas, S.G., 2008b. Late Cenozoic vertebrate fossil assemblages from Jalisco, Mexico. *New Mexico Mus. Nat. Hist. Sci. Bull.* 44, 51–64.
- Marcus, L.F., Berger, R., 1984. The significance of radiocarbon dates for Rancho La Brea. In: Martin, P.S., Klein, R.G. (Eds.), *Quaternary Extinctions: A Prehistoric Revolution*. The University of Arizona Press, Tucson, Arizona, pp. 159–183.
- Martin, J.M., Mead, J.I., Barboza, P.S., 2018. Bison body size and climate change. *Ecol. Evol.* 8, 4564–4574. <https://doi.org/10.1002/ece3.4019>.
- Martínez-Navarro, B., Pérez-Claros, J.A., Palombo, M.R., Rook, L., Palmqvist, P., 2007. The Olduvai buffalo *Pelorovis* and the origin of *Bos*. *Quater. Res.* 68, 220–226. <https://doi.org/10.1016/j.yqres.2007.06.002>.
- Martínez-Navarro, B., Ros-Montoya, S., Espigares, M.P., Palmqvist, P., 2011. Presence of the asian origin bovini, *hemibos* sp. aff. *Hemibos gracilis* and *Bison* sp., at the early Pleistocene site of venta micena (Orce, Spain). *Quat. Int.* 243, 54–60. <https://doi.org/10.1016/j.quaint.2011.05.016>.
- Masini, F., Palombo, M.R., Rozzi, R., 2013. A reappraisal of the early to middle Pleistocene Italian bovidae. *Quat. Int.* 288, 45–62. <https://doi.org/10.1016/j.quaint.2012.03.026>.
- McDonald, J.N., 1981. *North American bison: Their Classification and Evolution*. University of California Press, p. 316.
- McDonald, J.N., Lammers, G.F., 2002. *Bison antiquus* from Kenora, Ontario, and notes on the evolution of North America Holocene *Bison*. In: Emry, R.J. (Ed.), *Cenozoic Mammals of Land and Sea: Tributes to the Career of Clayton E. Ray*. Smithsonian Contributions to Paleobiology, No. 93. Smithsonian Institution Press, Washington, DC, pp. 83–97.
- Metcalfe, S.E., Leng, M.J., Kirby, J.R., Huddart, D., Vane, C.H., Gonzalez, S., 2016. Early-mid Pleistocene environments in the Valsequillo Basin, Central Mexico: a reassessment. *J. Quat. Sci.* 31, 325–336. <https://doi.org/10.1002/jqs.2851>.
- Mooser, O., Dalquest, W.W., 1975. Pleistocene mammals from aguascalientes, central Mexico. *J. Mammal.* 56 (4), 781–820.
- Nielsen, E., Gryba, E.M., Wilson, M.C., 1984. *Bison* remains from a Lake Agassiz spit complex in the Swan River valley, Manitoba: depositional environment and

- paleoecological implications. *Can. J. Earth Sci.* 21, 829–842. <https://doi.org/10.1139/e84-089>.
- Osborn, H.F., 1905. Recent vertebrate paleontology. Fossil mammals of Mexico. *Science* 21, 931–932.
- Palacio, P., Berthonaud, V., Guérin, C., Lambourdière, J., Maksud, F., Philippe, M., Plaire, D., Stafford, T., Marsolier-Kergoat, M.-C., Elalouf, J.-M., 2017. Genome data on the extinct *Bison schoetensacki* establish it as a sister species of the extant European bison (*Bison bonasus*). *BMC Evol. Biol.* 17, 48. <https://doi.org/10.1186/s12862-017-0894-2>.
- Palombo, M.R., 2016. Large mammals faunal dynamics in southwestern Europe during the late early Pleistocene: implications for the biochronological assessment and correlation of mammalian faunas. *Alpine and Mediter. Quat.* 29, 143–168.
- Pavia, M., Zunino, M., Coltorti, M., Angelone, C., Arzarello, M., Bagnus, C., Bellucci, L., Colombero, S., Marcolini, F., Peretto, C., Petronio, C., Petrucci, M., Pieruccini, P., Sardella, R., Tema, E., Villier, B., Pavia, G., 2012. Stratigraphical and palaeontological data from the early Pleistocene pirro 10 site of pirro nord (puglia, south eastern Italy). *Quat. Int.* 267, 40–55. <https://doi.org/10.1016/j.quaint.2010.12.019>.
- Pichardo, M., 1997. Valsequillo biostratigraphy: new evidence for Pre-Clovis date. *Anthropol. Anzeiger* 233–246.
- Pichardo, M., 1999. Valsequillo biostratigraphy II. Bison, tools, correlate with Tequixquiac. *Anthropol. Anzeiger* 57, 13–24.
- Ramsey, C.B., Lee, S., 2013. Recent and planned developments of the program OxCal. *Radiocarbon* 55, 720–730. <https://doi.org/10.1017/s0033822200057878>.
- Rivals, F., Semperebon, G.M., 2012. Paleoindian subsistence strategies and late Pleistocene paleoenvironments in the northeastern and southwestern United States: a tooth wear analysis. *J. Archaeol. Sci.* 39, 1608–1617. <https://doi.org/10.1016/j.jas.2011.12.039>.
- Rivals, F., Soloumias, N., Muhlbacher, M.C., 2007. Evidence for geographic variation in the diets of late Pleistocene and early Holocene *Bison* in North America, and differences from the diets of recent *Bison*. *Quater. Res.* 68, 338–346. <https://doi.org/10.1016/j.yqres.2007.07.012>.
- Sánchez Salinas, M., Jiménez Hidalgo, E., Castañeda Posadas, C., 2016. Fossils of Pleistocene mammals from the area of san mateo huexoyucan, tlaxcala, Mexico. *Bol. de La Soc. Geol. Mexicana* 68 (3), 497–514.
- Scopoli, I.A., 1777. *Introductio ad historiam naturalem sistens genera lapidum, plantarum, et animalium. Hactenus detecta, characteribus essentialibus donata. Tribus Divisa, Subinde Ad Leges Naturae.* Gerle, Prague, p. 506.
- Shapiro, B., Drummond, A.J., Rambaut, A., Wilson, M.C., Matheis, P.E., Sher, A.V., Pybus, O.G., Gilbert, M.T.P., Barnes, I., Binladen, J., Willerslev, E., Hansen, A.J., Baryshnikov, G.F., Burns, J.A., Davydov, S., Driver, J.C., Froese, D.G., Harington, C.R., Keddie, G., Kosintsev, P., Kunz, M.L., Martin, L.D., Stephenson, R.O., Storer, J., Tedford, R., Zimov, S., Cooper, A., 2004. Rise and fall of the Beringian steppe bison. *Science* 306, 1561–1565.
- Skinner, M.F., Kaisen, O.C., 1947. The fossil *Bison* of Alaska and preliminary revision of the genus. *Bull. Am. Mus. Nat. Hist.* 89, 123–256.
- Solorzano, F., 2002. Localidades y fauna fósil registrada para el Estado de Jalisco, vol. 9. Reporte Técnico del Instituto Nacional de Antropología e Historia, Jalisco.
- Stevens, R.E., Metcalfe, S.E., Leng, M.J., Lamb, A.L., Sloane, H.J., Naranjo, E., González, S., 2012. Reconstruction of late Pleistocene climate in the Valsequillo Basin (Central Mexico) through isotopic analysis of terrestrial and freshwater snails. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 319–320, 16–27. <https://doi.org/10.1016/j.palaeo.2011.12.012>.
- Szabo, B.J., Malde, H.E., Irwin-Williams, C., 1969. Dilemma posed by uranium-series dates on archaeologically significant bones from Valsequillo, Puebla, Mexico. *Earth Planet Sci. Lett.* 6, 237–244. [https://doi.org/10.1016/0012-821X\(69\)90163-0](https://doi.org/10.1016/0012-821X(69)90163-0).
- Van der Made, J., 2013. First description of the large mammals from the locality of Penal, and updated faunal lists for the Atapuerca ungulates - *Equus altidens*, *Bison* and human dispersal into Western Europe. *Quat. Int.* 295, 36–47. <https://doi.org/10.1016/j.quaint.2012.03.001>.
- Van Zyll de Jong, C.G., 1986. A systematic study of recent bison, with particular consideration of the wood Bison (*Bison bison athabasca* rhoads, 1898). *Publ. Nat. Sci.* 6, 1–69.
- Vekua, A., 1995. Die Wirbeltierfauna des Villafranchium von Dmanisi und ihre biostratigraphische Bedeutung. *Jahrb. Des. Romisch-Germanischen Zentralmus. Mainz* 42, 77–180.
- Vercoutère, C., Guérin, C., 2010. Les bovidae (mammalia, artiodactyla) du Pleistocene moyen final de l'aven de Romain-la-Roche dous France). *Rev. Paleobiol.* 29, 655–696.
- Villada, M.M., 1903. Acerca de la fauna fósil del valle de México, vol. 7. *Anales del Museo Nacional de México, Primera Época*, pp. 441–451.
- Wilson, M., 1974. The Casper local fauna and its fossil bison. In: Frison, G.C. (Ed.), *The Casper Site: A Hell Gap bison Kill on the High Plains.* Eliot Werner Publications, pp. 125–171.
- Wilson, M.C., Hills, L.V., Shapiro, B., 2008. Late Pleistocene northward-dispersing *Bison antiquus* from the bighill creek formation, gallelli gravel pit, alberta, Canada, and the fate of *Bison occidentalis*. *Can. J. Earth Sci.* 45, 827–859. <https://doi.org/10.1139/E08-027>.
- Woodburne, O., 2004. *Late Cretaceous and Cenozoic Mammals of North America.* Columbia University Press, Chichester, New York, p. 391.