Pleistocene record of mammals and pollen from Mexico (Las Tazas, Valsequillo, Puebla) and their paleoenvironmental interpretation

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ABSTRACT

The Valsequillo paleontological area in Puebla has been widely explored and several fossil localities are studied with the presence of megafaunal and micromammal remains. It has been suggested the possible presence of humans by indirect evidence from Pleistocene outcrops. Despite being a site of great paleontological interest, the geology of the area is complex and poorly defined, mainly at a local scale. We present the new Late Pleistocene locality Las Tazas, Valsequillo, Puebla, Mexico, which is located in Barranca Caulapan, bearing megafaunal remains and fossil pollen material. Twenty-two megafaunal elements and 32 fossil pollen samples were recovered from the same stratigraphic layer. The collected fossil material was deposited in the Paleontological Collection of the Benemérita Universidad Autónoma de Puebla. The fossil mammal remains represent the orders Cingulata, Perissodactyla, Artiodactyla, and Proboscidea; the families Pampatheriidae, Equidae, Bovidae, Camelidae, and Elephantidae; the genera *Pampatherium, Equus, Bison, Camelops,* and *Mammuthus;* and the species *Pampatherium mexicanum, Equus conversidens, Camelops hesternus,* and *Mammuthus columbi*. The fossil pollen of the genera *Pinus* and *Quercus* is identified; as well as pollen related to grasses (e.g., Poaceae, Asteraceae, and Amaranthaceae). The presence of *Bison* allows us to infer a Late Pleistocene-Early Holocene age for the fossil association. Las Tazas is the fossil locality with the greatest paleodiversity in the state of Puebla. Palynological analyses indicate a paleoenvironment of grasslands with *Pinus* and *Quercus* open forests and the presence of water bodies.

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INTRODUCTION

The biological diversity in Mexico is mainly explained by the great climatic variation that prevails in the region, due to both its latitude and longitude location and its orography, which generate temperate and tropical conditions that converge in the central part of the country (Challenger and Soberón, 2008; Ferrari et al., 2012). The central part of Mexico shows a complex vegetation pattern resulting from its ecological and geological history (Mastretta-Yanes et al., 2015).

In Mexico, changes in the floristic and faunal composition during the Pleistocene are documented at high elevations (Trans-Mexican Volcanic Belt [TMVB], Sierra Madre Oriental, and Sierra Madre Occidental); they were generated by (cold) glacial and (warm) interglacial episodes at higher elevations (Arroyo-Cabrales et al., 2005). During these glacial and interglacial periods the dispersion of vertebrate fauna occurred (Ceballos et al., 2010; Ferrusquía-Villafranca et al., 2010), resulting in an extensive record of large mammals from studies carried out from the 1950s to the present day (Armenta, 1959; Pérez-Crespo et al., 2009; Ceballos et al., 2010; Ferrusquía-Villafranca et al., 2010; Castañeda Posadas, 2015; Castañeda-Posadas et al. 2022).

The state of Puebla is located in the TMVB and near Puebla city. The Valsequillo Basin has the highest number of Pleistocene mammals recorded in the state (Arroyo-Cabrales et al., 2005; Ferrusquía-Villafranca et al., 2010; Castañeda-Posadas, 2015; Herrera Flores, 2017). The Valsequillo area is an interesting locality because there is a record of the presence human at the end of the Pleistocene (Pichardo 1997; VanLandingham 2004; Huddart et al., 2008; González et al., 2006, 2015).

Despite the extensive megafaunal evidence in Mexico, the paleobotanical record is scarce. Metcalfe et al. (2016) reported the presence of Pleistocene pollen and diatoms from Valsequillo suggesting that the region was covered by lake or a water body surrounded by pine forest (Straka and Ohngemach, 1989; VanLandingham, 2006). Other paleoenvironmental reconstructions have been based on stable isotope analyses in megafaunal remains and continental snails (VanLandingham, 2006; Stevens et al., 2012; Pérez-Crespo et al., 2014; Metcalfe et al., 2016) suggesting the presence of grasslands and open forests. However, as is the case with paleontological studies of the Pleistocene of Mexico, fossil studies in vertebrates are independent of paleobotanical micropaleontological studies. Therefore, this study presents the record of the Pleistocene mammals from Las Tazas, Valsequillo Basin, Puebla, linking the information between the megafauna and fossil pollen record, and combining paleontological efforts to substantially complement the paleoenvironmental interpretation.

GEOLOGICAL SETTING

The locality Las Tazas, Junta Auxiliar de Santo Tomás Chautla, Puebla, is located in "18°57´06.3" N, "98°08´08.9" W, at 2076 m a.s.l. (Figure 1), southern Puebla City, the capital of the state.

The oldest rocks in the area include an early Cretaceous limestone beneath sediments of the Balsas Group, mainly Eocene-Oligocene red conglomerates (Pichardo, 1997). The Pleistocene strata are composed of basaltic tuff and lava spills (named Zacachimalpa or Caulapan, lakes bed or Ixcalco lava by González et al., 2006). However, most of these sediments consist of volcanic deposits with sandy-carbonate clay and carbonated silt deposited in large basins to a lesser extent (Castañeda-Posadas, 2015). The upper strata are composed of igneous rocks (intermediate and acid
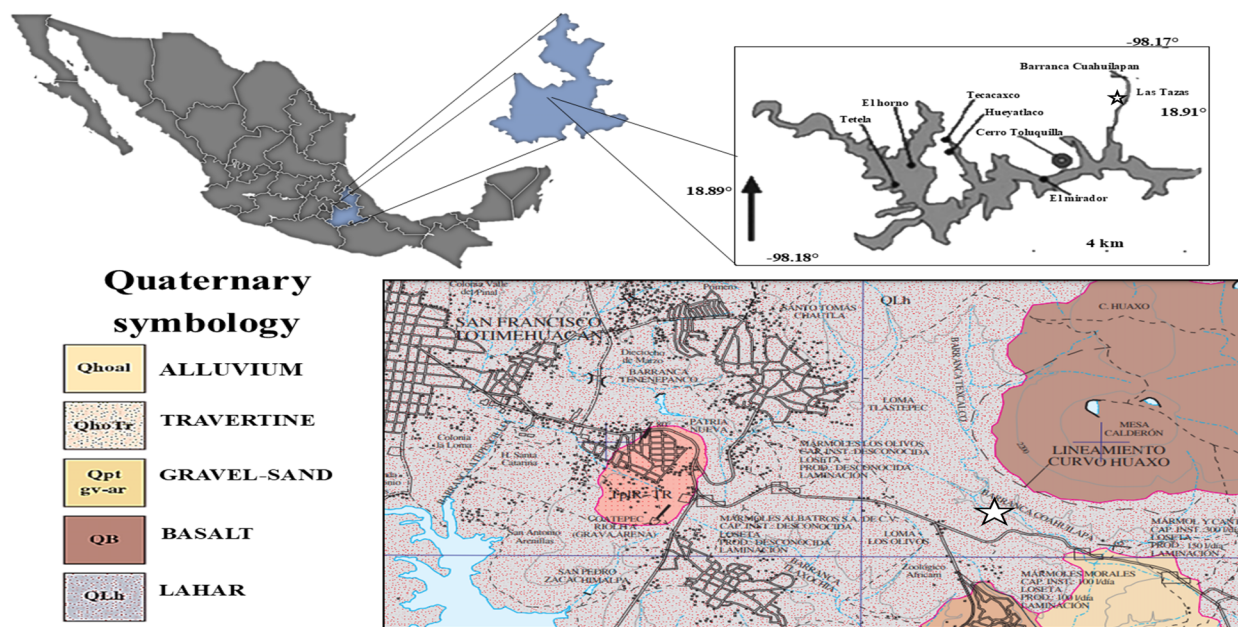
FIGURE 1. Location of Las Tazas site (white star) near to Valsequillo lagoon in the middle of Puebla State, and the location of the fossil site in a regional geological map (Servicio Geológico Mexicano, 2014; 1:50 000).

tuffs, andesites, basalts, and volcaniclastics) and sedimentary rocks (limestones, sandstones-conglomerates, conglomerates, and siltstones-sandstones) of Pleistocene age (Jiménez-Hidalgo et al., 2015), where several mammal and human fossils have been found (González et al., 2006).

Las Tazas site is located on the western slope of Barranca Caulapan, where lacustrine, fluvial, and volcanic ash deposits known as *Valsequillo gravels*. The estimated age from Barranca Caulapan is between 38.9 and 7,151 ^{14}C years before present (González et al., 2006; Díaz-Sibaja et al., 2020). The stratigraphic column of Las Tazas includes, from the base to the top, a brown silt with clay, silts with conglomerate lens, brown silt with fine sands, conglomerate with presence of fossil mammals, green silts and ashes, and finally a black paleosol (Figure 2).

MATERIAL AND METHODS

A systematic excavation was conducted for the extraction of fossils (Viñas-Vallverdú et al., 2015), which were packed and transported in field jackets for their protection. The pollen samples from the sediments of the fossil-bearing strata and each sample was placed in hermetic plastic bags, which were individually labeled for their transportation. The stratigraphic column of Las Tazas was made in SedLog 3.1 (Zervas et al., 2009). The entire process of cleaning, stabilization, and reconstruction of specimens and the preparation of palynological material were done at the Paleontology Laboratory of the Benemérita Universidad Autónoma de Puebla (BUAP). We did the extraction of palynomorph following the procedure proposed by Martinez-Hernández, et al. (1980).

A total of 22 megafaunal fossil elements were identified corresponding to four orders, five families, five genera, and six species (Table 1, Figure 3), as well as pollen records of the genera *Pinus*, and *Quercus*, and herbaceous (e.g., Poaceae, Asteraceae, and Amaranthaceae). Both megafaunal and pollen specimens were deposited in the Paleontology Laboratory rof BUAP (BUAPAL). Megafaunal fossils were identified using specialized literature (e.g., Skinner and Kaisen 1947; Schmid, 1972; Von den Driesch, 1976; Sisson and Grossman, 1978; Gillette and Ray, 1981; Dixon, 1993; Adams and Crabtree, 2001; Lopez Bejar et al., 2008; Campos-Camacho, 2012; Góis Lima, 2013) and compared to remains housed at BUAPAL and the Paleontological Collection of the Centro INAH-Puebla (CRINAHP). Palynomorphs were identified using specialized literature (Chavez and Rzedowski, 1993; Perveen, 1999; Van Wichelen et al., 1999; Flores-Cruz et al., 2006).

SYSTEMATIC PALEONTOLOGY

Superorder XENARTHRA Cope, 1889
Order CINGULATA Illiger, 1811
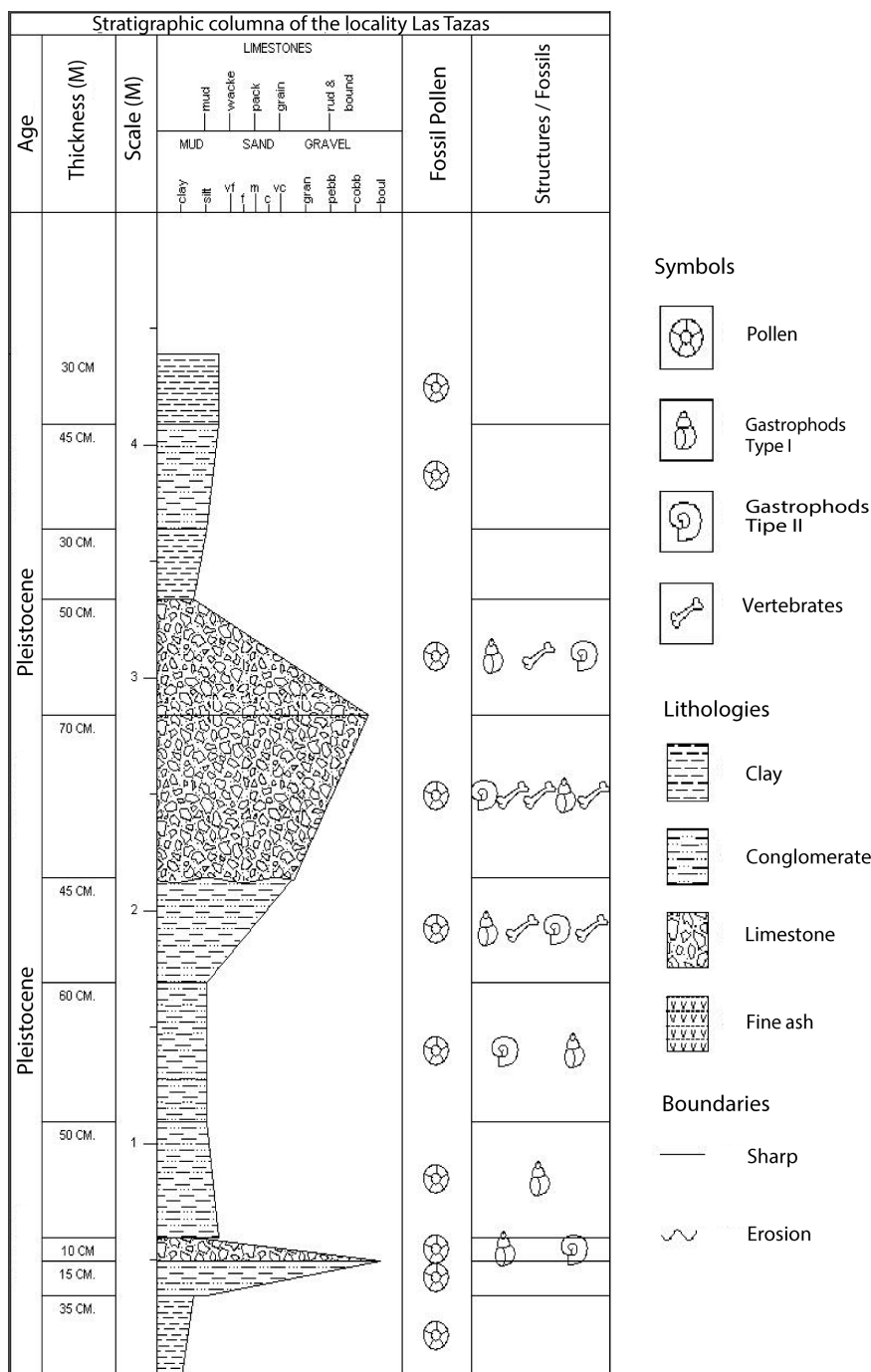
FIGURE 2. Stratigraphic column of the locality Las Tazas, Valsequillo, Puebla, indicating the layer with the fossil verte-brate materials.

Family PAMPATHERIIDAE Paula Couto, 1954
Genus *PAMPATHERIUM* Gervais and Ameghino, 1880
Pampatherium mexicanum Edmund, 1996

Referred material. One movable osteoderm (der-mal bony plate) (BUAPAL 768; Figure 3A), mov-able osteoderm fragment (BUAPAL 767; Figure 3B), and two fixed scapular shields (BUAPAL 769 and 779; Figure 3C–D).

Description. The complete movable osteoderm (BUAPAL 768) has a rectangular shape with three sections (Montellano-Ballesteros, 1991). The lower part (45 mm) has a series of shallow foramina in the lower margin. The middle part (30 mm) is

TABLE 1. Megafauna and fossil pollen taxa identified in the locality Las Tazas.

Mammals			Pollen		
Order	Family	Species	Order	Family	Genus
Xenarthra	Pampatheriidae	*Pampatherium mexicanum*	Pinales	Pinaceae	*Pinus*
Perissodactyla	Equidae	*Equus conversidens, Equus* sp.	Fagales	Fagaceae	*Quercus*
Artiodactyla	Bovidae	*Bison* sp.			
	Camelidae	*Camelops* cf.*C. hesternus*			
Proboscidea	Elephantidae	*Mammuthus columbi*			

rugose and has a 35 mm long curvature at the attachment near the upper part; this latter part is completely smooth (Montellano-Ballesteros, 1991; Aguilar and Laurito, 2009; Góis Lima, 2013).

The movable osteoderm fragment (BUAPAL 768) only has the upper part (25 mm), with a rectangular shape, reticulations on the anterior articular surface, and a series of dots on the sculpted surface, mainly on the contour of the surface. The fixed osteoderms (BUAPAL 769 and 779) from the scapular region have a poorly marked ornamentation composed of multiple small pores, its marginal elevation is flattened or diffuse, and the longitudinal depressions are superficial.

Comparison and remarks. The family Pampatheriidae is represented in Mexico by two genera, *Pampatherium* and *Holmesina*. This family is characterized by diagnostic osteoderms that allow the distinction between the two genera (Edmund, 1996; Scillato-Yané et al., 2005). *Pampatherium mexicanum* is the only recognized species of this genus in North America (Mead et al., 2007). Movable osteoderms in the genus *Pampatherium* are poorly ornamented, the marginal band may be absent, particularly in the Mexican population, or may consist of a narrow band of follicular pores on the posterior part and the lateral margins; the marginal band is not significantly depressed under the submarginal band and in the central part is broad, low, and without protrusions or a raised keel (Edmund, 1996), which are characteristics observed in the fossil material from Las Tazas.

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Order PERISSODACTYLA Owen, 1848
Family EQUIDAE Gray, 1821
Genus *EQUUS* Linnaeus, 1758
Equus conversidens Owen, 1869

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Referred material. Left M2 (BUAPAL 773; Figure 3E), right M3 (BUAPAL 774; Figure 3F).

Description. The measurement of left M2 and right M3 are: length (Al) = 24.6 mm, transversal width (Tw) = 23.81 mm and Al =24.33 mm, Tw =19.31 mm. Both molars present the enamel well , and its occlusal configuration can be observed,

where the lingual edge of the protocone is moderately concave, the enamel folding on the outer edge of the fossettes is simple and deep, the caballing fold is simple, faint in upper left M2 and strongly developed in upper right M3.

Comparison and remarks. The structures observed in the fossils BUAPAL 774 and 773 as observed in *E. conversidens*; (Reynoso-Rosales and Montellano-Ballesteros, 1994; Sánchez Salinas et al., 2016; Priego-Vargas et al., 2017). The values presented in this work are within the variation of *E. conversidens* and *E. excelsus* (Table 2), this species are smaller in size than *E. mexicanus* but are larger than *E. cedralencsis* and *E. francisi*. However, there are qualitative differences that help to separate both species, such as the lion edge of the protocone, which is more concave in *E. excelsus* than in *E. conversidens*; the folding of the enamel on the external edge of the pliprotoloph and plihypostyle pits are absent in *E. excelsus* and present in *E. conversidens*. The variation in size and occlusal characteristics of molars in equids has allowed the identification of at least five species associated in three groups of equids for the Mexican territory (Reynoso-Rosales and Montellano-Ballesteros, 1994; Sánchez-Salinas et al., 2016; Priego-Vargas et al., 2017).

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Equus sp.

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Referred material. Left mandible with three complete deciduous premolars dp2, dp3, and dp4 (BUAPAL 780; Figure 3I–J), right p3 (BUAPAL 771; Figure 3G), and left m2 (BUAPAL 772; Figure 3H).

Description. The left hemimandible has three deciduous premolars that are slightly worn. The length of the dp2 to dp4 is approximately 100 mm. The molariform p3 and m2 have an Al = 24.0 mm, Tw = 13.04 mm, Al = 22.4 mm, and Tw = 14.47 mm, respectively.

Comparison and remarks. The values of the dp2 to dp4 is within the variation of length of p2-p4 of adults *E. mexicanus* p2-p4 length = (86.99–109.95 mm), instead the other species of Pleistocene adult horses the maximum value of p2-p4 length is 92.6
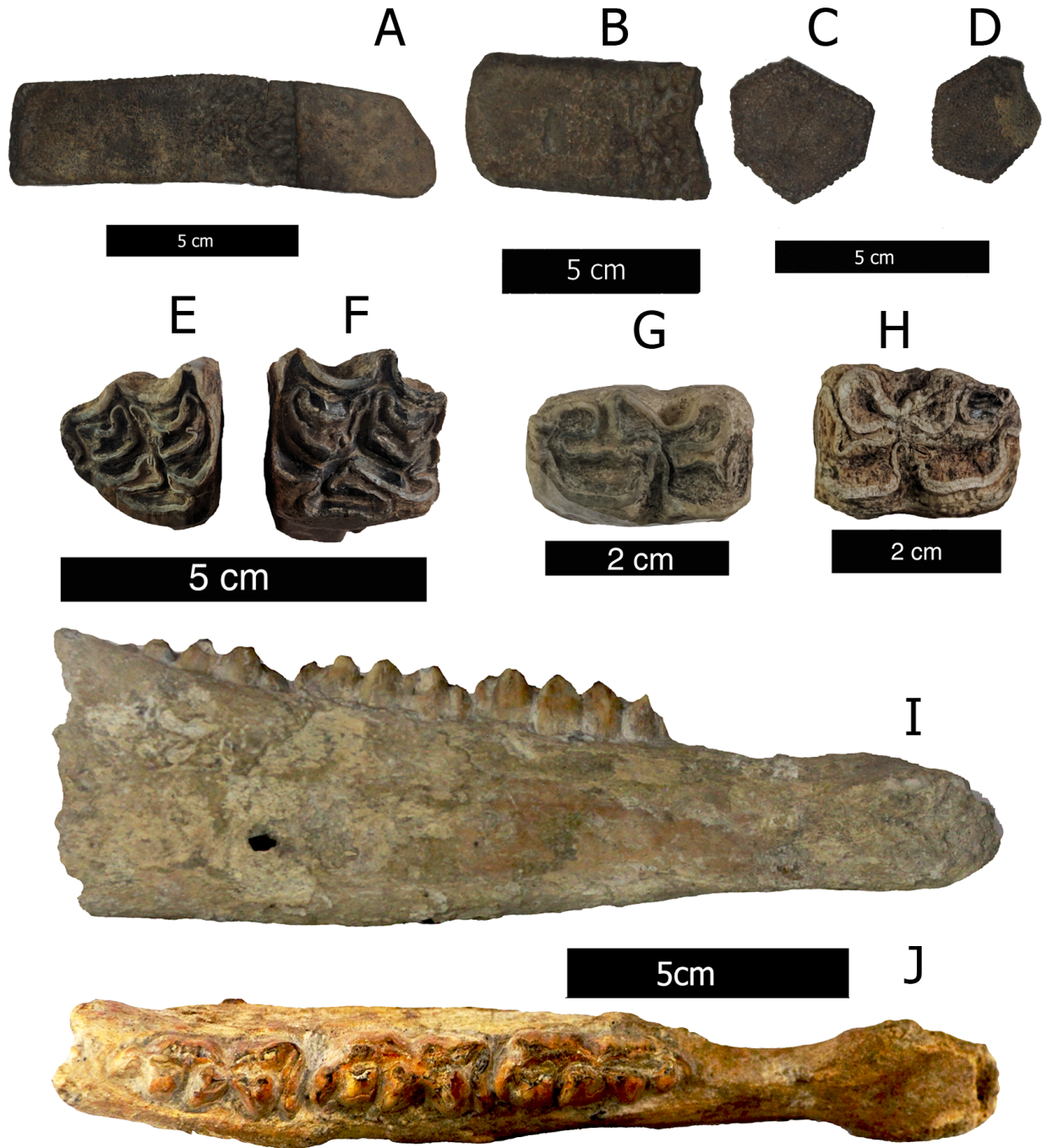
FIGURE 3. Fossil material of pampathere and horses from Las Tazas, Valsequillo, Puebla. *Pampatherium mexicanum*: **A**, movable osteoderm (BUAPAL 768); **B**, movable osteoderm fragment (BUAPAL 767); **C**, fixed scapular shield (BUAPAL 769); **D**, fixed scapular shield (BUAPAL 779). *Equus conversidens*: **E**, left M2 (BUAPAL 773); **F**, right M3 (BUAPAL 774). *Equus* sp.: **G**, right p3 (BUAPAL 771); **H**, right m2 (BUAPAL 772); **I–J**, left mandible (BUAPAL 780). Figures A–D in dorsal view; E–H and J in occlusal view; I in labial view.

mm (Priego-Vargas et al., 2017) (Table 3). Jiménez-Hidalgo et al. (2019) describe a jaw of a juvenile *E. mexicanus* with deciduous premolars with a length of the dp2 to dp4 =120 mm from Chiapas, Mexico. The juvenile specimen from Chiapas is larger than BUAPAL 780 and because the teeth of juvenile individuals do not present diagnostic

TABLE 2. M2 and M3 measurements in fossil *Equus conversidens* found in Las Tazas locality (BUAPAL) compared with other species of *Equus* and *Haringtonhippus* reported in Mexico by Priego-Vargas et al. (2017). All measurements are in millimeters.

Species	Anteroposterior length			Transverse width		
	Mean	Min–Max	N	Mean	Min-Max	N
M2						
BUAPAL 773	—	24.6	1	—	23.81	1
E. mexicanus	29.65	26.35–31.50	6	28.18	25.80–31.40	6
E. conversidens	22.75	20.50–25.80	32	22.54	19.79–24.20	32
H. francisci	19.55	18.10–20.50	4	18.28	16.37–20.00	4
M3						
BUAPAL 774	—	24.33	1	—	19.31	1
E. mexicanus	31.35	27.5–36.33	6	24.89	23.30–27.80	6
E. conversidens	23.85	21.50–27.45	32	19.51	17.10–23.70	32
H. francisci	22.45	21.60–23.05	3	15.53	14.00–17.30	3

characters to separate between species of horses, we determine the fossil material to genus level.

The molariforms are smaller than *E. mexicanus*, and its measurements are within the ranges of *E conversidens* and *E. cedralensis*. The molariforms exhibit advanced deterioration on the occlusal surface, but the prefosette and postfosette are visible. In the right p3 the u-shaped linguaflex, possibly pointed metastyle, entoconid possibly square and almost absent equine fold. The left m2 presents a v-shaped linguaflex, apparently round entoconid and # aballing fold. Several qualitative occlusal characters do not fall into the description reported for small horses in the literature (Sánchez-Salinas et al., 2016; Priego-Vargas et al., 2017), therefore we determine the fossil material to genus level.

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Order ARTIODACTYLA Owen, 1848
Family BOVIDAE Gray, 1821
Genus *BISON* Hamilton Smith, 1827
Bison sp.

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Referred material. Cranium fragment with right horn core and lacking facial bones (BUAPAL 755, incomplete right mandible with a fragment of p3 and complete m1 to m3 (BUAPAL 756), complete molar M2 (BUAPAL 781), proximal scapula fragment (BUAPAL 761), a fragment of the proximal epiphysis of the right ulna (BUAPAL 754), an almost complete left metacarpus (BUAPAL 764), right talus (BUAPAL 763), fragment of cervical vertebra (BUAPAL 762), and two lumbar vertebrae (BUAPAL 758 and 759); Figure 4.

Description. The cranium fragment (BUAPAL 755) retains part of the left and right frontal from the orbital fossa to the occipital condyle. The right horn

TABLE 3. Measurements of the p2-p4 premolars of *Equus* spp. and the sum of their means (taken from Table 3, Priego-Vargas et al., 2017).

Species	Anteroposterior length of pm 2-3		
M2	Mean	Min–Max	N
BUAPAL 773	—	100.00	1
E. mexicanus	101.1	94.90–105.00	13
E. conversidens	84.0	77.30–91.40	18
H. francisci	71.7	70.10–71.70	4

core has a length of 200 mm, an internal length of 230 mm, an external length of 295 mm from tip to base, a circumference of 290 mm, a diameter of 100 mm, and an estimated total horn core length from tip to tip (TLTT) of 700 mm.

Comparison and remarks. These horn measurements and the horn cores laterally directed are within the variation of *B. antiquus* (Table 4) (Lucas, 1899; Skinner and Kaisen, 1947; Von den Driesch, 1976; McDonald, 1981; Díaz-Sibaja et al., 2020). *B. occidentalis* despite presenting horn nuclei that moved backwards (Díaz-Sibaja et al., 2020) is considered synonymous of *B. antiquus* based on ancient DNA studies that demonstrated that both are the same anagenetic lineage (Shapiro et al., 2004; Wilson et al., 2008).

The M2 (BUAPAL 781) has a length = 33.41 mm and a width = 22.06 mm. The occlusal surface is badly damaged, it presents a well-developed entostyle, the fossettes have the characteristic U shape with some folds, and the wear of the molar indicates it belonged to an adult. The incomplete right mandible presents a fragment of pm3 and complete m1, m2, and m3 (BUAPAL 756); the molars are hypsodont with well-developed ento-
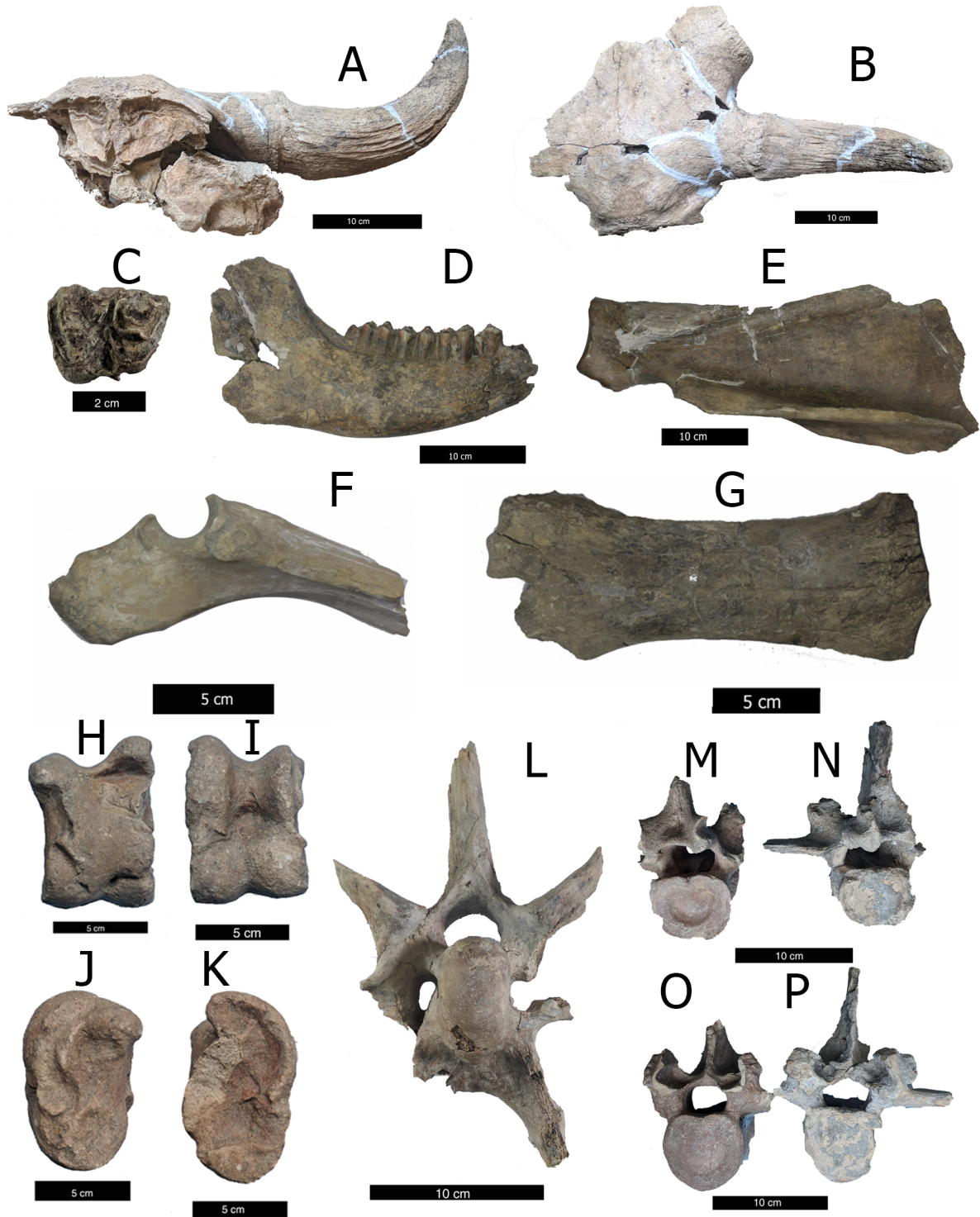
FIGURE 4. Fossil material of bison from Las Tazas, Valsequillo, Puebla. *Bison*: **A–B**, cranium fragment (BUAPAL 755); **C**, molar M2 (BUAPAL 781); **D**, right mandible (BUAPAL 756); **E**, right scapula (BUAPAL 761); **F**, right ulna (BUAPAL 754); **G**, left metacarpus (BUAPAL 764); **H–K**, right astragalus (BUAPAL 763); **L**, cervical vertebra (BUAPAL 762); **M–N**, lumbar vertebra (BUAPAL 758); **O–P**, lumbar vertebrae (BUAPAL 759). Figures A in occipital view; C in occlusal view; I, L, N, and P in anterior view; B, E, and G in dorsal view; D, F, and K in lateral view; J in medial view; H, M, and O in posterior view.

TABLE 4. Cranial measurements comparison between the fossil material from Las Tazas, Valsequillo (BUAPAL) and the *Bison* species reported by McDonald (1981) and Skinner and Kaisen (1947). LTPP = total length of the horn cores from end to end, DVCC = vertical diameter of the horn cores and their circumference, LRC = relative length of the horn core, ACO = width between the occipital condyles. All measurements are in millimeters.

Species	LTPP		DVCC		LRC	
	Min–Max	N	Min–Max	N	Min–Max	N
BUAPAL 755	700	1	100	1	200	1
B. antiquus	765–1067	27	81–126	27	203–364	27
B. occidentalis	626–1055	77	70–114	85	186–392	86
B. bison	510–778	128	69–99	139	124–270	134
B. latifrons	1445–2235	19	107–178	34	551–1090	25
B. athabascae	542–848	9	81–106	9	165–323	9
B. priscus	751–1064	23	84–116	52	285–416	36
B. alaskensis	800–1540	25	100–153	49	426–795	36

style, and the shape of the molars are sharp in lateral view with light wear. All of these traits are characteristics of genus *Bison* (Allen, 1876; Chandler, 1916; Hillson, 2005).

A fragmented right scapula (BUAPAL 761) presents the glenoid fossa with a diameter = 88 mm, the internal border of the scapula has a length = 165 mm, and the total length of the scapula is 430 mm. It is observed that the area immediately dorsal to the glenoid and bordered by the mid-neck ridge and posterior margin is markedly thinned and flattened, which is characteristic of the genus *Bison* (Von den Driesch, 1976; McCuaig-Balkwill and Cumbaa, 1992; France, 2008; Raymond and Prothero, 2011). The scapula belongs to an adult individual according to the measurements reported by Von den Driesch (1976), McCuaig-Balkwill and Cumbaa (1992), and France (2008).

The ulna is fragmented (BUAPAL 754), it presents a fracture in the diaphysis, the proximal region is preserved with a flattened and well-defined olecranon, with the major cavity in semilunate shape. The curvature of the olecranon has a depth of 14 mm. All these features and the ulna not fused with the radius indicate that the specimen was a juvenile (Ritz and Wing, 2008).

Left metacarpus (BUAPAL 764) is wider and slightly shorter, characteristic observed in *Bison* (McDonald, 1981; Skinner and Kaisen, 1947) and its measurements (Table 5) are close to those of *B. antiquus* (McDonald, 1981; McCuaig-Balkwill and Cumbaa, 1992). The articular condyle of the left metacarpal IV (BUAPAL 764) lacks distal epiphysis and it is close to *B. antiquus* (McDonald, 1981; Baskin, et al., 2022). However, we do not

have diagnostic characteristics to assign it to specific level.

The right calcaneus (BUAPAL 763) shows the lateral articular surface of the distal trochlea covering the distal surface, the tubercle is at the same line with the dorsal portion, features of the genus *Bison* (McCuaig-Balkwill and Cumbaa, 1992).

The sixth cervical vertebra (BUAPAL 762) has well-defined caudal and cranial regions, the rostral condyle is convex with a rounded margin, the medullary canal is present; the articular process is wide with a rounded margin, the cranial articular process is flat and incomplete, the transverse processes are flat, large, and present a triangular shape, the articular processes are damaged, and the angle between the lateral branches of the transverse process is wider and deeper, similar to features present in *Bison* (McCuaig-Balkwill and Cumbaa, 1992).

The lumbar vertebrae (BUAPAL 758, 759) are almost complete. They exhibit a compression of the vertebral body in the cranial and caudal regions. The cranial region has a height = 52 mm, which is the same as the width of the facies = 52 mm. In the caudal region, the vertebrae present a width in the facies = 59 mm and the length of the vertebrae = 73 mm; the dorsal margin of the anterior articular process is at the same level than the upper part of the articular facet, characteristics observed in *Bison* (McCuaig-Balkwill and Cumbaa, 1992). The fossil material was determined to belong to an adult individual because of the similarity with the measurements reported by Von den Driesch (1976) and Skinner and Kaisen (1947).

All postcranial remains are assigned to *Bison* sp. because they exhibit the morphological charac-

TABLE 5. Metacarpal measurements comparison between the fossil material from Las Tazas, Valsequillo (BUAPAL) and the *Bison* species reported by McDonald (1981) and Skinner and Kaisen (1947). L = total length of bone, AP = Antero-posterior minimum of diaphysis, TRtr = Transverse minimum of diaphysis. All measurements are in millimeters.

Species	L		AP		TRtr	
	Min–Max	N	Min–Max	N	Min–Max	N
BUAPAL	207	1	27	1	44	1
B. antiquus	211–238	28	28–33	28	47–61	28
B. occidentalis	248–300	150	29–38	161	32–48	156
B. bison	232–276	118	27–34	115	30–34	115
B. latifrons	270–281	3	32–34	3	38–41	3
B. athabascae	256–279	4	30–35	5	34–39	5

teristics of this genus (McDonald, 1981) but is very difficult separate species into this genus with post-cranial material. Ancient DNA analyzes with 405 remains of *Bison* aged between 60,000 and recent, demonstrated broad genetic diversity in populations during the Late Pleistocene that are mainly subdivided into four major clades, showing that all *Bison* sequences are closely related and are not indicative of multiple and independent species (Wilson et al., 2008). Due to the similarity of the isolated horn nuclei and postcranial elements of *B. antiquus* and *B. occidentalis*, identification of Late Pleistocene and early Holocene *Bison* should be made with caution (Wilson et al., 2008).

Family CAMELIDAE Gray, 1821
Genus *CAMELOPS* Leidy, 1854
Camelops cf. *C. hesternus* Leidy, 1873

Referred material. Left calcaneus (BUAPAL 757), Figure 5.

Description. The left calcaneus (BUAPAL 757) is robust, with a length = 158 mm, body width = 68 mm, interior curvature = 35 mm, and belongs to an adult individual since the epiphyses are well fused without a trace of the sutures (Reitz and Wing 2008).

Comparison and remarks. Unlike other artiodactyls of similar size, such as the genus *Bison*, the cuboid articular facet is wider, the distal astragalar surface is divided into a medially oriented distal part and an anteriorly oriented proximal part, the articular surface of the fibula is convex proximally and concave distally, and the proximally positioned groove is shallower than in *Bison* (Guérin and Faure, 1999; Zazula et al., 2016). The family Camelidae in Valsequillo during the Late Pleistocene is represented by *Camelops, Hemiauchenia,* and *Paleolama*. We can exclude an assignment of BUAPAL 757 to *Hemiauchenia* because this genus is smaller (Table 6). *Camelops* and *Paleolama* are of similar size, but *Camelops* is more robust which

FIGURE 5. Fossil material of camel and mammoth from Las Tazas, Valsequillo, Puebla. *Camelops* cf. *C. hesternus*: **A–B**, left calcaneus (BUAPAL 757). *Mammuthus columbi*: **C**, left femur (BUAPAL 775). Figure A in medial view; B in lateral view; C in caudal view.

TABLE 6. Calcaneal measurements comparison between the fossil material from Las Tazas, Valsequillo (BUAPAL) and the Camelidae species reported by Guérin and Faure (1999) measurements are in millimeters.

Species	Maximun length		Maximun anteroposterior length		Tuber transverse width		Tuber anteroposterior width	
	Min–Max	N	Min–Max	N	Min–Max	N	Min–Max	N
BUAP 757	168	1	67	1	35	1	54	1
C. hesternus	157.0–170.0	13	65.0–76.7	13	40.5–53.2	13	56.4–65.3	13
H. cf. *H. macrocephala*	122.6–125.6	12	52.3–53.7	12	—	—	—	—
–	103.0–116.5	12	30.5–35.5	4	24.5–28.0	7	33.0–39.5	7

Order PROBOSCIDEA Illiger, 1811
Family ELEPHANTIDAE Gray, 1821
Genus *MAMMUTHUS* Brookes, 1828
Mammuthus columbi Falconer, 1858

Referred material. Left femur (BUAPAL 775), Figure 5.

Description. The femur presents the greater and lesser trochanters well defined, the internal and external femoral condyles are also present, as well as the fossette in lesser trochanter region. It has a long body with a length =1300 mm, with well-defined proximal and distal regions with a width = 230 mm and 280 mm, respectively, and a slender diaphysis.

Comparison and remarks. Therefore, the characters mentioned above correspond to the genus *Mammuthus,* since the other two proboscidean families (Mammutidae and Gomphotheriidae) have expanded distal condyles medial and laterally and the robustness of the femur is less than in mastodon but is greater than gomphotheres, particularly on the shaft and medial condyle, and the femur of these families is smaller in size (Tapia-Ramírez et al., 2013). *M. columbi* is the only valid mammoth species of the Late Pleistocene in Mexico (Lister and Sher, 2015). *M. columbi* is the largest proboscidean in Mexico, it has a wide distribution in North America with more than 270 localities in central Mexico (Agenbroad, 2005; Arroyo-Cabrales et al., 2010).

PALYNOLOGICAL ANALYSIS

Ten samples of sediment were taken from the different layers in the study site (Figure 2), recovering a total of 38 palynomorphs. The dominant groups identified belong to genera *Pinus* (with 48%) and *Quercus* (with 52 %). However, the genera *Amaranthus, Fraxinus, Mimosa, Ulmus,* and *Salix* also appear, as well as representatives of the family Olaceae and Asteraceae (Figure 6).

The pollen diagram shows variation along the stratigraphic column in the dominance of floristic elements and in the arboreal and herbaceous elements (Figure 6). The basal layers of the sequence show a greater presence of the genera *Pinus* and *Quercus*, suggesting the presence of other tree groups and a temperate forest. Subsequently, in the sequence from 115 to 230 cm deep, where the bone-bearing stratum is found, the arboreal groups are getting scarcer, and the herbaceous groups and plants associated with water bodies dominate. In the stratum above 115 cm, the dominance of a closed forest reappears, and the portion of creeping plants, and plants associated with water bodies decreases.

The results suggest the variation In the conditions and floristic associations, in the basal is a temperate forest (of *Pinus* and *Quercus)*, but later it becomes more grassland (Amarantaceae and Asteraceae) and presence of water bodies as suggested by the presence of the genera *Fraxinus*, *Ulmus*, and *Mimosa*.

DISCUSSION

Interdisciplinary studies of the fossil record are fundamental to analyze the possible changes in the flora and fauna throughout geological time, the response of biotic communities to climate change, and extinction events (O'Keefe et al., 2023). Specific information about the extinctions, diversification processes, and paleodistribution during the Pleistocene can be obtained from Mexico (Ferrusquía-Villafranca et al., 2017) due that ?800 localities with presence of fossil mammals have been recorded across the Mexican territory (Ferrusquía-Villafranca et al., 2010). Valsequillo Basin is a fossiliferous area with the most representative Late Pleistocene fauna of the state of Puebla (Jiménez-Hidalgo et al., 2015), and various studies have been conducted in this place (González et al., 2006). The continuous discovery of fossil material in this locality allows a better
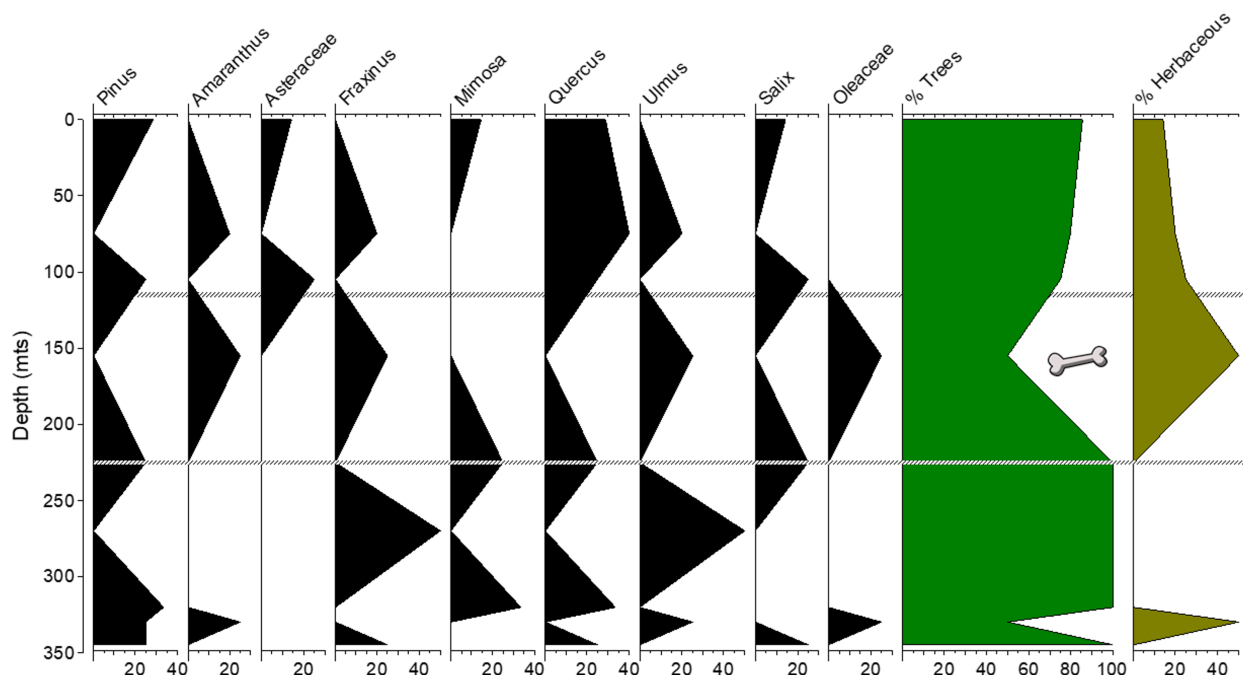
FIGURE 6. Pollen diagram of the locality Las Tazas, Valsequillo, Puebla, Mexico. Showing on the right in dark green the arboreal elements vs in light green the herbaceous elements. Area delimited by grey lines indicates the layers with the presence of vertebrate remains (bone silhouette). Diagram was made in Tilia 3.0.1.

understanding of both plants and animals and the different structures of the Pleistocene communities, as well as contributing information that can be compared with paleobiological patterns present in other regions (Jiménez-Hidalgo et al., 2015).

The locality Las Tazas in the Valsequillo area is characterized by its distinct diversity of Pleistocene mammals, including artiodactyls (*Bison* sp. and *Camelops hesternus*), proboscideans (*Mammuthus*), equids (*Equus conversidens*, *Equus* sp.), and pampatheriids (*Pampatherium mexicanus*), which correspond to a Rancholabrean association, consistent with previous reports (Ceballos et al., 2010; Ferrusquía-Villafranca et al., 2010, 2017). In addition, the inclusion of the plant species emphasizes the heterogeneity of the vegetation present in the surroundings of this locality. In the megafauna-bearing stratum, the identified pollen allows inferring a vegetation composed of a semi-open mixed forest composed mainly of pines and oaks (Lozano-García et al., 2014) and the genus *Salix* indicates the presence of water bodies in the region (García-Ortega and Belmonte Soler, 2008). Open-type vegetation with a water body nearest to site in low areas and more closed plant communities in elevated areas, were available for herbivores with mixed diets, thus showing heterogeneity in vegetation and species derived fauna associated with food diversity (Louys et al., 2011). For exam-

ple, the presence of grasslands, *Amaranthus*, and Asteraceae is associated with the faunal record of bisons, mammoths, and horses; on the other hand, shrub areas with presence of *Pinus, Fraxinus, Mimosa, Quercus, Ulmus,* and *Salix* can be associated with camels (Green et al., 2005; Pérez-Crespo et al., 2009; Stevens et al., 2012).

There are few studies documenting the plant paleodiversity of the state of Puebla, and it was until the end of the 1980s when Straka and Ohngemach (1989) conducted a palynological analysis in the basin of the Mexican highland, considered the first palynological record for Puebla, reporting the presence of *Alnus, Carpinus, Carya, Junglans, Ulmus, Fraxinus, Liquidambar,* and *Fagus,* which is confirmed with that recorded by Stevens et al. (2012). The latter authors mention that, at approximately 20 000 YBP, the climate of Valsequillo was colder and may have been drier compared to present-day conditions, and thus the species would have had to adapt to the changing climatic conditions. Metcalfe et al. (2016) report the presence of pines and woody shrubs, as well as shallow lakes, according to the pollen found, which allows making an association with the present pine-oak vegetation where the megafauna inhabited. This association of forest patches and increased water availability is supported by records of angiosperm

wood such as *Cordia, Dalbergia,* and *Prioria* (Sainz-Reséndiz, 2011).

Therefore, the study of palynological material allows to infer patterns about the population dynamics of the vegetation present in the locality Las Tazas in an effective way as along as presence data are related to similar localities (Ferrusquía-Villafranca et al., 2010). The importance of this locality with respect to the association of the flora and fauna present, compared to the localities in central Mexico, lies in the diversity of species with the same specific ecological requirements, which suggests that the organisms belonged to the same community (Herrera Flores, 2017).

Many studies referring to the area of Valsequillo show the great diversity of species that have been identified over more than half a century (Arroyo-Cabrales et al., 2005; Armenta, 1959; Cruz-Muñoz, 2009; Ferrusquia-Villafranca et al., 2010; Castañeda- Posadas, 2015; Bravo-Cuevas et al., 2016; Herrera Flores, 2017), but they were initially carried out without a systematic collection of information and are mainly based on material collected in the 1960s that lacks stratigraphic data. In contrast, in the present study, we were able to obtain as much information as possible on the stratigraphy and both plant and animal diversity of the Late Pleistocene in a specific area of Valsequillo, Puebla.

CONCLUSIONS

During the Late Pleistocene, the megafauna dominated the landscape of the locality Las Tazas and was part of the Pleistocene ecosystems of Valsequillo, with a great diversity of organisms.

The Pleistocene landscape of Las Tazas was dominated by herbivores associated with the vegetation structure, which was composed of trees *(Pinus* and *Quercus)* and an herbaceous stratum (Oleaceae, *Mimosa*, Asteraceae [Compositae]).

The landscape inferred for the locality Las Tazas a tree assemblage composed of a temperate-humid forest with open areas and bodies of water. The megafauna that inhabited the landscape of Las Tazas was characteristic of Pleistocene ecosystems dominated by large herbivores, grazers and browsers.

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