



**UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
PROGRAMA DE POSGRADO EN CIENCIAS DE LA TIERRA
INSTITUTO DE GEOLOGÍA**

**RECONSTRUCCIÓN DE LOS PAISAJES PRESENTES EN MÉXICO
DURANTE EL PLEISTOCENO TARDÍO A TRAVÉS DEL ESTUDIO DE
SECUENCIAS EDAFOGÉNICAS ALUVIALES.**

T E S I S

QUE PARA OPTAR POR EL GRADO DE
DOCTORA EN CIENCIAS DE LA TIERRA

PRESENTA:
ROSA ELENA TOVAR LICEAGA

COMITÉ TUTOR:
Dr. Sergey Sedov (Director), Instituto de Geología, UNAM
Dra. Marisol Montellano Ballesteros, Instituto de Geología, UNAM
Dr. Lorenzo Vázquez Selem, Instituto de Geografía, UNAM

JURADO EXAMINADOR:
Dr. Sergey Sedov, Instituto de Geología, UNAM
Dra. Marisol Montellano Ballesteros, Instituto de Geología, UNAM
Dr. Alexander Correa-Metrio, Instituto de Geología, UNAM
Dra. Emily McClung de Tapia, Instituto de Investigaciones Antropológicas,
UNAM
Dra. Berenice Solís, Centro de Investigaciones en Geografía Ambiental, UNAM

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A MI ESPOSO

A MIS HIJOS: ÓSCAR Y NAOMI

A MIS PADRES

Y A TODOS AQUELLOS QUE SIEMPREN HAN ESTADO

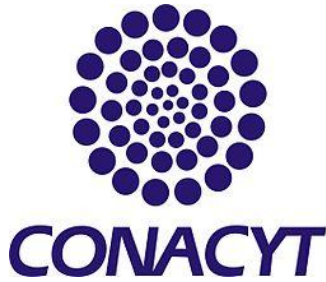
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Abstract

México is in the fifth place of megadiversity in the world. However during the Pleistocene the biota was more diverse.

This work presents the results of paleoenvironmental proxies studied in two areas: Santa Cruz Nuevo and Axamilpa, both in the south of Puebla. Both localities correspond to the end of marine isotopic stages 3 and 2 (MIS 3 and MIS 2) and bring fossils previously studied.

Four pedostratigraphic units were recognized in Santa Cruz Nuevo (stagnogleyic, calcic, gley and humic). Between the units, fluvial sediments were identified and correspond to channels and lenses. The radiocarbon ages (30380 ± 220 ^{14}C years BP (34512 ± 191 cal. years BP) in paleosol 8Bg and 31680 ± 120 ^{14}C years BP (35610 ± 403 cal. years BP) in paleosol 3A) place the formation of paleosols at the end of MIS 3. The isotopic signatures in the first three units correspond to C3 plants however the fossils are not in concordance. The vertebrate fossils suggest dry ecosystems as xeric shrublands, spiny forests, and grassland. Few fossil elements suggest forests which are colder and wetter. In order to explain this incongruence, it is suggested a dominance of CAM plants (-13 to -23) which isotopic signature varies according to water availability.

The environmental conditions during MIS 3 are similar to Present in Santa Cruz with the exception of megafauna.

Axamilpa is 50 km away from Santa Cruz Nuevo and includes the end of MIS 3 and MIS 2, being younger than Santa Cruz Nuevo. In Axamilpa, fossil findings correspond to megafauna.

Four pedostratigraphic units were recognized (gley, vertic, calcic and humic) with isotopic signatures of -22.6 to -24.7 . The phytoliths suggested contrasting conditions with the other locality, which is older. In here, the abundance of coniferous

phytoliths indicates humid and cold conditions at the end of MIS 3. These conditions changed, becoming drier and warmer because the presence of C4 grasses and changed again during the formation of calcic unit.

In the calcic unit the increment of coniferous phytoliths and C3 grasses suggests a recovery of the forest but with some grass patches. The last unit, the humic, is wetter and probably drier because grass phytoliths.

This pattern of climatic oscillations can be correlated with other national records of the same age but not with other countries because the regional factors as topography, mineralogy and biotic plasticity.

The holistic vision would help to explain the Pleistocene dynamics and the role that the climatic oscillations play in the extinction and extirpation of species in Mexico.

Resumen

México ocupa el quinto lugar en biodiversidad actual. Se ha mencionado que durante el Pleistoceno la biodiversidad de Norteamérica debió ser mayor a la actual. Sin embargo hasta fecha reciente se ha puesto énfasis en conocer la dinámica de los ecosistemas durante el Pleistoceno tardío.

En este trabajo se reconstruyen las condiciones ambientales reinantes al final del Pleistoceno tardío, MIS 3- MIS 2, en el sur de Puebla: Santa Cruz Nuevo y Axamilpa a través del uso de diferentes proxies. En ambas localidades existen fósiles de vertebrados terrestres que se han estudiado de forma preliminar.

En Santa Cruz Nuevo se reconocieron cuatro unidades pedoestratigráficas con base en sus características macroscópicas (estagnogleyca, cálcica, gleyca y húmica). Entre y dentro de las distintas unidades se identificó sedimentación fluvial que corresponde principalmente a lentes o pequeños canales. Las edades de radiocarbono (30380 ± 220 ^{14}C años AP (34512 ± 191 años cal. AP) en el paleosuelo 8Bg y 31680 ± 120 ^{14}C años AP (35610 ± 403 años cal. AP) en el paleosuelo 3A) ubican a la localidad al final de la MIS 3. Las firmas isotópicas son bastante constantes a lo largo de la secuencia (unidades estagnogleyca, cálcica y gleyca) con valores promedio de -22 a -23, con excepción de la unidad húmica donde las firmas isotópicas son ligeramente más positivas, alrededor de -19. Estos valores indican una predominancia de plantas con metabolismo C3 que es característico de ambientes húmedos. Sin embargo, la fauna no indica dominancia de ecosistemas C3. El análisis de los análogos actuales sugiere que las asociaciones faunísticas se desarrollaron principalmente en ecosistemas secos (matorral xerófilo, bosque espinoso, pastizal). Existen pocos elementos característicos de ecosistemas templados (bosque de encino, bosque de coníferas). Para explicar esta aparente contradicción se deduce que las plantas dominantes debieron tener

metabolismo CAM cuyo rango isotópico abarca desde -13 hasta -23 y donde la respuesta isotópica de las plantas varía con respecto a la disponibilidad de agua.

Las condiciones ambientales al final de la MIS 3 son muy similares a las actuales en Santa Cruz Nuevo y zonas aledañas. La gran diferencia radica en la biota, con extirpación de especies y la extinción de la megafauna.

La localidad de Axamilpa, se localiza a 50 km de la de Santa Cruz Nuevo. Esta localidad es más joven que la de Santa Cruz Nuevo abarcando la parte final de la MIS 3 e inicios de la MIS 2. En dicha secuencia se reconocieron cuatro unidades pedoestratigráficas (gleyca, vértica, cálcica y húmica) donde el rango de los valores de isótopos estables de carbono recuperados varía entre -22.6 a -24.7 , lo cual indicaría una mayor presencia de plantas C3 a todo lo largo del perfil. El análisis de fitolitos permite diferenciar las comunidades dominantes de plantas. Al final de la MIS 3 se estableció un bosque de coníferas lo cual es indicativo de condiciones húmedas y frías. Posterior a dicho evento, las condiciones se tornaron más secas estableciéndose patrones vérticos. Se observó una disminución fuerte de fitolitos de coníferas y un aumento significativo de fitolitos de gramíneas, particularmente de C4 que soportan condiciones más secas que los C3 y que son característicos de ecosistemas cálido-secos. La unidad cálcica presenta condiciones más húmedas que la vértica con una pequeña recuperación del bosque. La unidad húmica presenta una biota de condiciones más húmedas que la anterior pero en condiciones probablemente más secas que la previa.

Estas pequeñas diferencias en la respuesta ambiental abrió la pregunta de si las secuencias pedoestratigráficas podrían estar respondiendo a cambios milenarios. La respuesta no es contundente. Debido al tiempo de formación del suelo y a la falta de un mayor control temporal es difícil hacer una correlación directa. Sin embargo, la existencia de asociaciones no-análogas y los suelos poligenéticos sugiere cambios

abruptos en las condiciones ambientales que no se pudieron asociar a ningún interglacial de Groenlandia o eventos Heinrich.

Los resultados muestran, a pesar de que la escala cronológica es vaga y de corta duración, intercalaciones entre condiciones húmedas y secas, correlacionables con otros registros nacionales de la misma edad.

La respuesta sin embargo varía de localidad en localidad debido a que es una respuesta a las condiciones locales que están influenciadas no solo por el clima sino también por otros factores como es la topografía, la mineralogía, la plasticidad de la biota, etc. Sin embargo, la visión holística en el estudio de localidades irá ampliando el conocimiento que se tiene sobre la dinámica de los ecosistemas de finales del Pleistoceno y el papel que jugaron las oscilaciones climáticas en la extinción y extirpación de especies.

Introducción

Principales registros paleoambientales, paleoclimáticos y paleoecológicos del Pleistoceno tardío

El Pleistoceno es uno de los periodos en los que se divide al Cuaternario. Se caracteriza por ciclos glaciales e interglaciales con una periodicidad de aproximadamente cada 100,000 años durante los últimos 800,000 años cuya causa se ha asociado a cambios orbitales (Milankovitch, 1920, 1941; Wolff *et al.*, 2010).

Hasta hace poco, la base del Pleistoceno (Figura 1) estaba definida hace aproximadamente 1.8 millones de años (m.a.) cerca de la cima del subcron Olduvai. Actualmente se define en aproximadamente 2.6 m.a., al final del cron Gauss (Gibbard *et al.*, 2008) debido a que es el inicio de las etapas glaciales (Ogg y Pillans, 2008). El límite entre el Pleistoceno y Holoceno se define hace 10 000 años de radiocarbono u 11,700 años calibrados antes del Presente (AP) (Gibbard y Kolfshoten, 2004). Presenta 103 etapas isotópicas marinas (MIS, por sus siglas en inglés).

La mayoría de las etapas isotópicas han sido reconocidas por la acumulación de loess, registro de núcleos de hielo, bandas orgánicas ricas de los sedimentos del Mediterráneo y otros estratos sensibles al clima (Gibbard *et al.*, 2008).

A últimas fechas se ha tratado de hacer una correlación entre los eventos marinos y terrestres, teniendo como problemas que las secuencias terrestres están altamente fragmentadas y son variables espacialmente. Sin embargo, la correlación directa se puede hacer a través de marcadores que estén presentes en ambos tipos de secuencias, como son los reversos magnéticos, fechamientos radiométricos, capas de tefra y rara vez en asociaciones fósiles (principalmente asociaciones polínicas) (Gibbard y Kolfshoten, 2004).

correlación entre la susceptibilidad magnética y el registro de isótopos de oxígeno (Maher y Thompson, 1999).

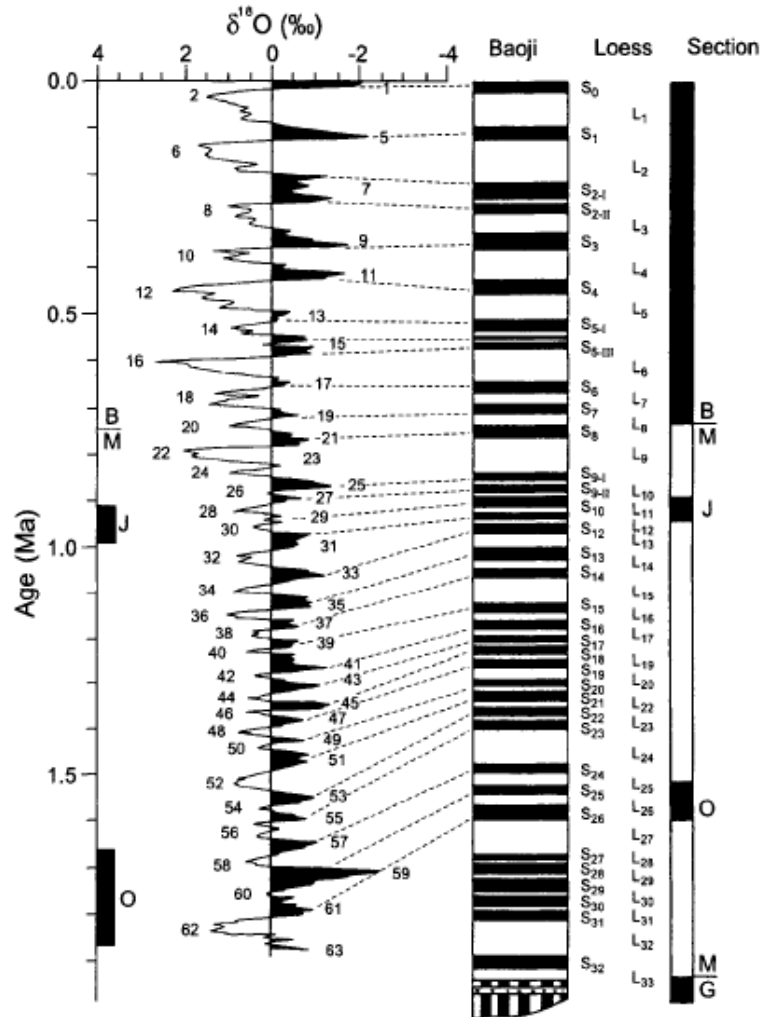


Figura 2. Comparación entre los registros de isótopos de oxígeno, con sus etapas indicadas y su correlación con la secuencia de loess-paleosuelos de Baoji, China. (Tomada de Bradley, 1999).

A escala suborbital, se ha observado una variabilidad climática milenaria durante el Último Glacial que abarca principalmente desde la MIS4 a la MIS2. Estas oscilaciones climáticas irregulares son conocidas como eventos Heinrich y ciclos Dansgaard-Oeschger (DO).

Los eventos Heinrich se reconocen por la presencia anómala de detritos acarreados por hielo (IRD, por sus siglas en inglés), transportados al océano por icebergs del hemisferio norte (Naughton *et al.*, 2009). Tienen una frecuencia de duración entre 1000-3000 años.

El depósito de las capas Heinrich se ha asociado con ciertos ciclos DO (Figura 3), sin embargo, muchos estadales Heinrich (HS, por sus siglas en inglés) tienen una duración menor a la del intervalo frío de Groenlandia (GS, estadales de Groenlandia) (Sanchez y Harrison, 2010).

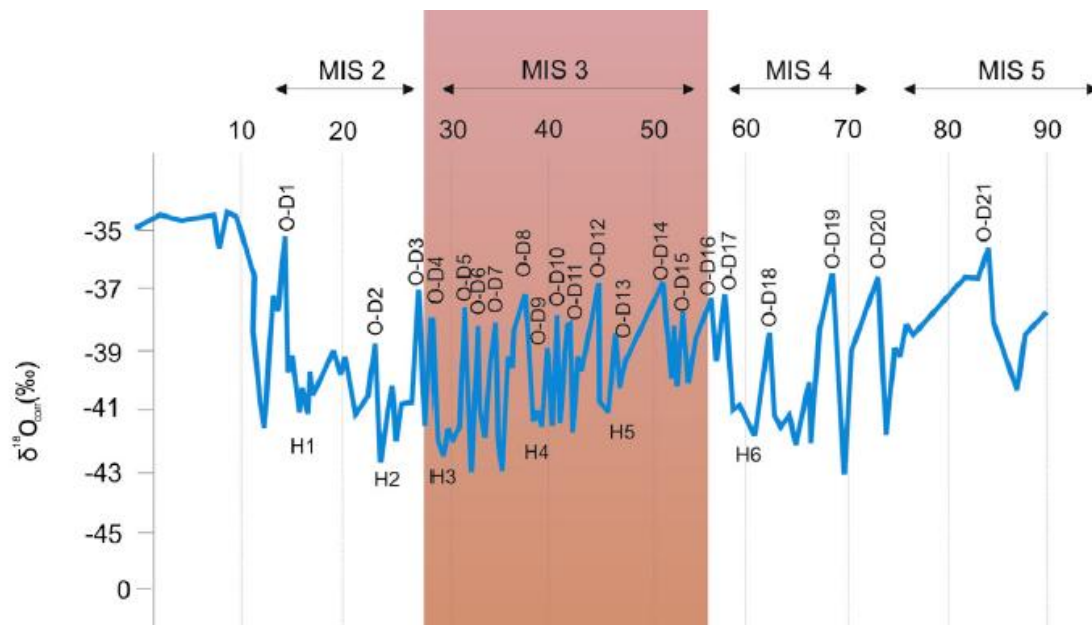


Figura 3. Identificación de ciclos DO y eventos H en el núcleo de hielo de Groenlandia. Extracto tomado de Rabassa y Ponce (2013).

Los ciclos DO han sido reconocidos en núcleos de Groenlandia como calentamientos abruptos seguidos de subsecuentes enfriamientos (Sanchez y Harrison, 2010). Se caracterizan por ser eventos cálidos con duración de años a décadas seguidos por enfriamientos graduales de cientos de años (Clark *et al.*, 2002). Los núcleos de hielo de Groenlandia revelan que cada ciclo DO inició con un calentamiento abrupto de un

estadial (GS) a un interestadial (GI) y que hubo enfriamientos graduales durante el inicio de cada fase interestadial para después entrar a un frío abrupto durante los estadales (Figura 4; Petersen *et al.*, 2013).

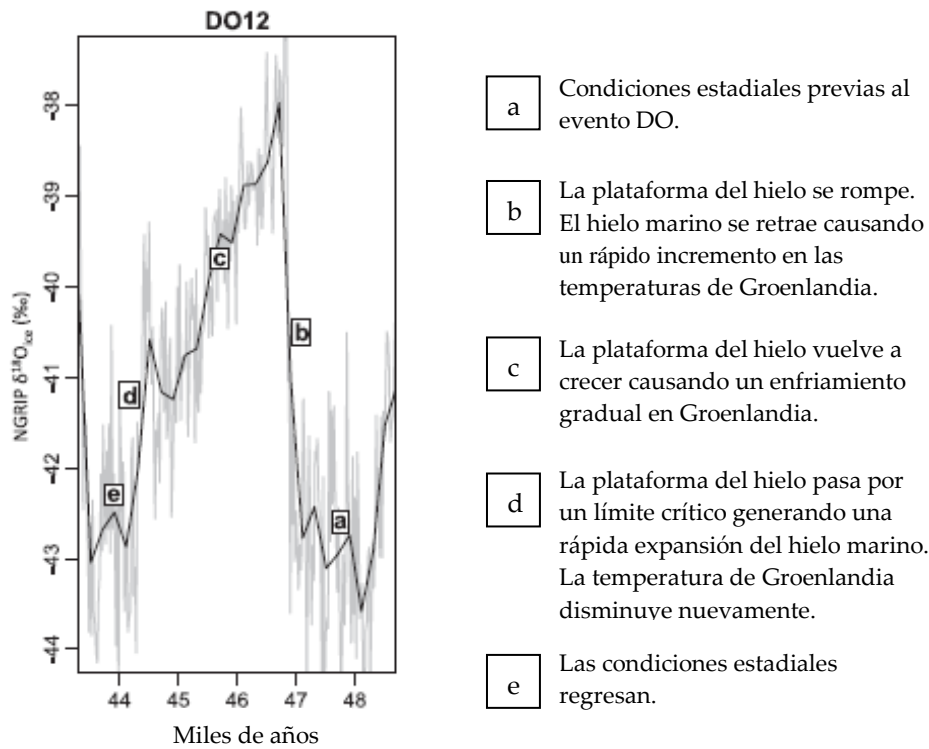


Figura 4. Propuesta del mecanismo de oscilación del ciclo Dansgaard-Oeschgaard.

Tomado de Petersen *et al.*, 2013

Hasta el momento se desconoce la causa que genera estas oscilaciones climáticas. Clark *et al.* (2002) y Lynch-Stieglitz *et al.* (2007) apuntan a que es consecuencia de la circulación termohalina global (THC, por sus siglas en inglés). La THC es la responsable del transporte del calor hacia los polos en el océano Atlántico.

Durante los eventos cálidos debió aumentar la tasa de evaporación y humedad atmosférica incrementando la salinidad del océano Atlántico y por tanto la circulación de la THC (Peterson *et al.*, 2000; Rabassa y Ponce, 2013) lo que debió provocar que la

zona de convergencia intertropical (ITCZ, por sus siglas en inglés) se desplazará hacia el norte (Hodell *et al.*, 2008).

Los eventos áridos coinciden con los eventos Heinrich cuando la zona de convergencia intertropical (ITCZ, por sus siglas en inglés) se desplazó hacia el sur (Hodell *et al.*, 2008) y el retorno meridional en el Atlántico (AMOC, por sus siglas en inglés) debió reducirse o alentarse provocando reducciones drásticas o totales de la convección de las aguas profundas del Atlántico norte (NADW, por sus siglas en inglés) (Elliot *et al.*, 2002).

La temperatura registrada en los hielos de Groenlandia muestra un patrón de condiciones más húmedas durante los interestadiales y secas durante los estadiales.

En diversos registros paleoambientales se observa, particularmente durante las etapas isotópicas marinas 3 y 2 estos cambios en las condiciones de humedad.

Registros paleoambientales-paleoclimáticos del Pleistoceno de México

La mayoría de los registros ya sean paleoclimáticos o paleoambientales en México provienen principalmente de estudios realizados en cuencas lacustres, paleosuelos, glaciales y recientemente a través de isótopos de oxígeno o carbono.

El registro glacial de México se centra principalmente en volcanes con elevaciones mayores a los 3800 msnm. Sin embargo, es el volcán Iztaccíhuatl el que tiene el registro glacial más completo debido a la ausencia de actividad durante el Pleistoceno tardío (Caballero *et al.* 2010; Vázquez-Selem y Heine, 2004).

Los avances glaciales de México se muestran en el Cuadro 1. Vázquez-Selem y Heine (2004) sugieren que las fluctuaciones glaciales observadas se debieron a cambios en temperatura y humedad durante el Pleistoceno mexicano.

Los registros muestran que durante los últimos 36,000-25,000 ¹⁴C años, en el centro de México existieron tres avances glaciares: el de la Malinche (Heine, 1988), Ajusco (White y Valastro, 1984; White, 1987), Hueyatenco I y II, ambos pertenecientes al Iztaccíhuatl (Caballero *et al.*, 2010; Vázquez-Selem y Heine, 2004). Durante estos avances en las localidades de Tlapacoya (González-Quintero, 1986; Watts y Bradbury, 1982) y Jalapasquillo (Straka y Ohngemach, 1989) reinaron las condiciones húmedas y frías con el establecimiento de bosques.

Sin embargo, varias localidades del centro-sur de México (Barranca Caulapan en Valsequillo, Puebla [isótopos $\delta^{18}\text{O}$ y $\delta^{13}\text{C}$ obtenidos de las conchas de caracoles terrestres], lagos de Chalco, Tecocomulco y Tlapacoya, los tres en el Estado de México, lago Cuitzeo, en Michoacán [capas de carbonatos, incremento de salinidad, diatomeas], Zacango, Nevado de Toluca, Estado de México y cuenca Zacapú, Michoacán [polen]) sugieren condiciones secas particularmente a partir de los 36,000 años A.P. hasta aproximadamente antes de los 23,000 años A.P., que es el inicio de la MIS 2 (Caballero

et al., 2001; Caballero-Miranda, 1997; Correa-Metrio *et al.*, 2012a; Israde-Alcántara *et al.*, 2002; Roy *et al.*, 2009; Stevens *et al.*, 2012; Watts y Bradbury, 1982).

Cuadro 1. Correlación de las cronologías glaciales de los volcanes de centro México.

Las edades están dadas en 14C antes del Presente, excepto donde están indicadas. Las edades de radiocarbono para la cronología del Iztaccíhuatl fueron estimadas usando CALIB.*

Iztaccíhuatl (Vázquez-Selem, 2000)	La Malinche (Heine, 1994, 1988)	Nevado de Toluca (Heine, 1994)	Ajusco (White y Valastro, 1984; White, 1987)
Ayoloco (< 1,265)	Rocas glaciares MV	Rocas glaciares MV	
	Rocas glaciares MIV (c. 3,500-2,000)	Rocas glaciares MIV (c. 3,500-2,000)	Neoglaciación I y II (< 2,000)
Milpulco-2 (c. 7400-6400)	MIII-3 (> 5,750)	Morrenas de MIII-3 y rocas glaciares (<11,500)	
Milpulco-1 (c. 10,000-9,000)	MIII-1 Y MIII-2 (10,000-9,000)	Morrenas de MIII-3 y rocas glaciares (<11,500)	
Hueyatlaco-2 (14,200-12,000)	MII (>15,000-12,000)	MI y MII (>11,500)	Albergue (<16,000->10,000)
Hueyatlaco-1 (c. 16,000-14,800)			Santo Tomás (>25,080) Marqués (>27,190)
	MI (36,000-32,000)		
Nexcoalango (195 ³⁶ Cl miles de años antes del Presente)	Pre-Wisconsiniano		

*Modificada de Vázquez-Selem y Heine, 2004

Los isótopos $\delta^{18}\text{O}$ y $\delta^{13}\text{C}$ obtenidos de las conchas de caracoles terrestres presentes en la Barranca Caulapan en Valsequillo, Puebla, indican que previo a los 36,000 ¹⁴C AP, el paleoclima era ligeramente más seco que en el presente. Después de ese intervalo, las condiciones ambientales se hicieron aún más secas hasta alrededor de los 20,000 ¹⁴C AP (Stevens *et al.*, 2012).

En Zacapu hay porcentajes relativamente altos de polen pertenecientes a las familias Poaceae, Asteraceae, Amaranthaceae y Cyperaceae lo que sugiere condiciones

secas (Correa-Metrio *et al.*, 2012a). Entre los 25,000-15,000 ¹⁴C al parecer no existió un cuerpo de agua debido a sedimentación baja (Ortega *et al.*, 2002) que Correa-Metrio *et al.* (2012a) asocia a las condiciones secas que prevalecieron desde hace más de 35,000 ¹⁴C años.

En otras localidades (lago de Texcoco y Valle de Teotihuacan) se han sugerido condiciones variables entre climas templados-subhúmedos con periodos secos (Lozano-García y Xelhuantzi-López, 1997). En Chalco y Tecocomulco se observa un patrón seco alrededor de los 27,000-25,000 ¹⁴C años (Caballero-Miranda, 1997; Caballero *et al.*, 2010; Roy *et al.*, 2009) y a partir de los 25,000 ¹⁴C años, las diversas cuencas lacustres que se localizan sobre la Faja Volcánica Transmexicana muestran cambios cíclicos entre condiciones húmedas y secas que se pueden registrar a escalas milenarias.

Torres-Rodríguez *et al.* (2015), haciendo uso de los carbonatos inorgánicos totales de un núcleo del Lago de Chalco, correlacionaron los registros de incendios a cambios milenarios. Concluyen que durante los periodos secos hubo una mayor concentración de carbonatos con respecto a lo normal. La mayoría de los incendios se dieron durante los periodos secos donde la mayor quema se detecta en la parte final de la MIS 3.

Las características geoquímicas de los sedimentos de diversas cuencas (Babícora (Roy *et al.*, 2012; 2013), Santiaguillo (Roy *et al.*, 2015), La Salada (Roy *et al.*, 2014) y Chalco (Lozano-García *et al.*, 2015)) sugieren que las variaciones hidrológicas fueron controladas por cambios ambientales milenarios. Se asocia el decremento en el corrimiento así como la mayor formación de carbonatos autigénicos a periodos secos que han asociado a ciertos eventos Heinrich.

Los estudios pedológicos (localidades de Nevado de Toluca, Estado de México, Huexoyucan, Tlalpan y Mammut, las tres en Tlaxcala) indican que las condiciones fueron frías y húmedas previo a los 29,000 años AP. (Sedov *et al.*, 2001; Sedov *et al.* 2009; Solís-Castillo *et al.*, 2012; Solleiro-Rebolledo *et al.*, 2011).

La etapa isotópica marina 2 es la mejor estudiada de todas ya que abarca el Último Máximo Glacial (UMG). Durante el UMG, la lluvia anual en el centro, sur y sureste de México debió disminuir en un 40 a 50% (Arroyo-Cabrales *et al.*, 2008). Para esta fase hay registro de glaciación en todas las montañas de más de 3800 msnm. Asimismo, estudios realizados en las cuencas interiores de la Faja Volcánica Transmexicana (lagos de Chalco, Texcoco, Tecocomulco, cuenca alta del Lerma, todas estas en el Estado de México, y los lagos de Cuitzeo y Zacapú, ambos en Michoacán), sugieren mayor aridez. En el centro-poniente y la península de Yucatán las condiciones fueron más húmedas (Caballero *et al.*, 1999; Caballero *et al.*, 2010; Sedov *et al.*, 2009), mientras que en algunas localidades de la región sur-centro (Barranca Caulapan en Valsequillo, Puebla, lago de Chalco Jalapasquillo, Puebla [polen], Tecocomulco, lago de Chignahuapan, Pátzcuaro) se registran condiciones de mayor humedad y menor temperatura en la parte superior de la MIS 2 (Bradbury, 2000; Caballero y Ortega, 1998; Metcalfe *et al.*, 2007; Stevens *et al.*, 2012; Straka y Ohngemach, 1989).

Estas fluctuaciones climáticas se debieron manifestar en las asociaciones bióticas ya que los organismos responden a los cambios en el ambiente.

Extinción de la megafauna durante el Pleistoceno

Hace 50,000 años, los ecosistemas a través del mundo estuvieron poblados por animales grandes que ahora están extintos. En todo el mundo, cerca de 90 géneros de animales con pesos superiores a los 44 kilos desaparecieron. El tiempo exacto de su desaparición varía de continente en continente sin embargo, alrededor de los 10,000 años estos animales se extinguieron excepto en latitudes muy altas, en islas y en África (Koch y Barnosky, 2006).

La causa o causas de la extinción de la megafauna al final del Pleistoceno siguen en debate (Cuadro 2). Lo que se sabe es que la mayor pérdida se dio en herbívoros y carnívoros de tamaño mediano a grande en Norte y Sudamérica, y Australia (Graham, 1986). Pocos géneros de micromamíferos se extinguieron aunque se perdió una gran cantidad de especies (Holman, 1995). En sí, sólo hubo extinciones de poblaciones locales de micromamíferos a varios niveles geográficos de forma simultánea a la megafauna debido al cambio de vegetación dado por el cambio climático (Martin y Neuner, 1978).

En Norteamérica, 34 géneros de mamíferos pleistocénicos de gran tamaño se extinguieron antes del Holoceno y 2 órdenes (Perissodactyla y Proboscidea) desaparecieron de forma regional. En Sudamérica, 50 géneros de megamamíferos se extinguieron y desaparecieron 3 órdenes (Notoungulata, Proboscidea y Litopterna) así como todos los xenartros gigantes. El norte de Eurasia perdió 9 géneros aunque existe duda de si los géneros de camello y bisonte se extinguieron o evolucionaron. Australia perdió 14 de sus 16 géneros de megamamíferos así como todos sus reptiles gigantes (6 géneros) y *Genyornis*, un ave no voladora gigante. Por el contrario, África casi no sufrió pérdidas, desapareciendo sólo 10 de sus géneros de megamamíferos (Cuadro 5; Koch y Barnosky, 2006).

Cuadro 2. Principales causas para la extinción de la megafauna al final del Pleistoceno.

Tomada de Koch y Barnosky (2006).

Tipo o nombre	Descripción
HIPÓTESIS AMBIENTALES	
Catástrofes	Megasequías, enfriamiento rápido, impacto de un bólido
Pérdida de hábitat	Los tipos de hábitat preferidos se perdieron o estaban muy fragmentados
Hipótesis de los nutrientes-mosaico	Pérdida de floras con alta diversidad local
Desequilibrio coevolutivo	Un rompimiento en las interacciones de coevolución entre plantas y animales debido a un rearrreglo en la flora
Inestabilidad auto-organizada	Colapso del sistema debido a una dinámica intrínseca
IMPACTOS HUMANOS DIFERENTES A LA SOBRECAZA	
Alteración del hábitat	Pérdida o fragmentación del hábitat debido a impactos humanos, incluyendo los incendios
Introducción de depredadores	Depredación directa por perros, ratas, gatos, puercos, etc.
Hiperenfermedad	Introducción de enfermedades virulentas
HIPÓTESIS DE LA SOBRECAZA	
Blitzkrieg	Pérdida rápida de presas debido a sobrecaza
Prolongación de la sobrecaza	Pérdida de presas debido a una interacción prolongada con el depredador
HIPÓTESIS COMBINADAS	

Megaherbívoros clave	Los ecosistemas colapsaron debido a la pérdida de la alteración del paisaje dada por los megaherbívoros, quizá con un incremento en los incendios
Cambio de presa	Los carnívoros no-humanos cambiaron de presa debido a que los humanos usurparon las que ellos usaban
Influencia del depredador	Los herbívoros se restringieron a refugios inviables

Cuadro 3. Porcentaje de extinción de géneros al final del Pleistoceno de forma global.

Tomada de Koch y Barnosky (2006).

	Número de géneros extintos de forma global	Número de géneros extintos que sobrevivieron en otros continentes	Número de sobrevivientes holocénicos	% Extinción
Norteamérica	28	6	13	72
Sudamérica	48	2	10	83
Eurasia	4	5	17	35
Australia	14	-	2	88
África	7	3	38	21

Faunas pleistocénicas de México

En México, aunque los sedimentos pleistocénicos están ampliamente distribuidos a lo largo del territorio, todavía falta conocer más acerca de la paleodiversidad así como de la distribución geográfica de los taxa. El registro de

mamíferos terrestres pleistocénicos consiste de 12 órdenes, 43 familias, 146 géneros y 278 especies de aproximadamente 800 localidades (Arroyo *et al*, 2002; Ferrusquía *et al*, 2010). Además existen 29 localidades con restos de aves y donde se han reconocido 98 géneros y 118 especies y de las cuales 17% son reportadas como extintas (Corona-M, 2002). Por último, 27 localidades presentan restos de herpetofauna con 10 géneros y 19 especies identificadas de anfibios sin especies extintas; y 29 géneros y 39 especies de reptiles con 4 especies extintas (Arroyo-Cabrales *et al*, 2008).

En el caso de México, la evidencia humana es muy escasa. De las casi 271 localidades mexicanas que contienen restos de mamuts, sólo 17 muestran relación con humanos. De estas localidades, 11 están perdidas o su localización actual es desconocida. Las restantes 5 están bien estudiadas (Arroyo-Cabrales *et al*, 2006).

Evidencias sugeridas de hombres tempranos en el Pleistoceno tardío de México incluyen restos humanos (González *et al*, 2003), líticos (Aveleyra Arroyo de Anda y Maldonado Koerdell, 1953; Aveleyra Arroyo de Anda, 1956), corazones (Lorenzo y Mirambell, 1981, 1986), posibles campamentos (Aveleyra-Arroyo de Anda, 1962), huesos modificados (Bárcena, 1882) y restos de fauna usada como comida (Aveleyra A. de Anda, 1956). Varias de estas evidencias han sido desechadas debido a que su origen pudo ser distinto al humano (Acosta-Ochoa, 2010).

Acosta-Ochoa (2010) menciona que los sitios que han sido datados con edades anteriores a los 12,000 años no son confiables y que la localidad mexicana más antigua reconocida corresponde a las cuevas inundadas de Yucatán que han sido estudiadas por González - González *et al*. (2008).

En el caso de las localidades analizadas en la Cuenca de México con restos de aves pleistocénicas, la evidencia, aunque se compone de pocos restos, sugiere que las poblaciones humanas más tempranas usaron a las aves de manera ocasional, de tal suerte que no hay rastros físicos en los restos que indiquen ese aprovechamiento.

Tampoco las evidencias alternativas, como la diversidad y el tamaño corporal de las aves, sugieren que estas fuesen utilizadas. (Corona-M., 2006).

Todos los datos anteriores confirman la presencia humana en México para el Pleistoceno tardío sin embargo, es poco probable que fueran los causantes de la extinción de las poblaciones de megafauna, al menos para México.

De hecho, la mayoría de los hallazgos de vertebrados pleistocénicos corresponden principalmente a depósitos aluviales que son más antiguos que la presencia humana en el país.

Registros aluviales, paleosuelos y fósiles

Los sistemas fluviales incluyen un amplio espectro de sedimentos generados por la acción de ríos y arroyos, donde el canal y el conjunto *overbank* o planicies de inundación (*floodplain*) comprenden el ambiente fluvial (Nichols, 2009).

Las planicies de inundación dan registro de los cambios en la hidrología y geomorfología del área a través de su arquitectura aluvial (Daniels, 2003). Han sido muy utilizadas por los investigadores que se enfocan a estudiar los cambios ambientales a través del tiempo ya que la sedimentación en las planicies de inundación depende del clima y de la distancia al canal activo. Las planicies de inundación frecuentemente se cubren y pueden preservar raíces, horizontes de suelo, restos de vertebrados e invertebrados, así como marcas de lodo y de lluvia (Prothero, 1990).

Las planicies de inundación no son un ambiente sedimentario uniforme. Las diferencias en las tasas de acreción, topografía y vegetación hacen que los paleosuelos asociadas a ellas sean muy heterogéneos. Las diferencias en las tasas de pedogénesis *versus* la acreción de la planicie de inundación resulta en un gran variedad de tipos de paleosuelos en diferentes etapas de maduración (Marriott y Wright, 1993; Smith, 1990).

Los paleosuelos de las planicies de inundación varían a varias escalas temporales y espaciales. Las variaciones laterales a microescala en la morfología de los paleosuelos en distancias de varias decenas a centenas de metros dan como resultado procesos locales asociados a inundaciones del *overbank*, de corta vida. Los cambios a mesoescala, definidos por variaciones a varios cientos a miles de metros de distancia desde el canal hacia la planicie de inundación (catenas y pedofacies) refleja procesos autogénicos como desbordamiento (*crevassing*) y agradación del *overbank* en cuencas inundadas locales. Los cambios a macroescala, definidos en escalas de varios kilómetros o decenas de kilómetros, reflejan procesos a gran escala, como avulsión de los canales del río y patrones más gruesos del drenaje de la planicie de inundación. La

variación de los paleosuelos a escala de cuenca es generalmente controlada por procesos alogénicos como cambios en el clima regional y actividad tectónica (Kraus, 2002).

Los suelos que se desarrollan sobre las planicies de inundación dejan evidencias claras de los cambios ambientales ocurridos, por ejemplo de la geomorfología del área (p. ej., gleysoles) o de las condiciones ambientales locales (p. ej., ferrisoles). Sin embargo, los rasgos macromorfológicos son solo una de las tantas pistas que dejan los suelos para las reconstrucciones ambientales.

Dentro de los elementos de la memoria edáfica que son usados en los suelos aluviales se cuenta el estudio de los isótopos de carbono dejados en la materia orgánica, restos de organismos o su actividad biótica (excretas o canales), restos perdurables de algunas plantas como son los fitolitos, registros de susceptibilidad magnética, entre otros.

También los restos fósiles de vertebrados terrestres que son comunes de hallar en secuencias aluviales proveen información de la fauna y por tanto de las relaciones bióticas del área.

Por todo lo anterior, los paleosuelos aluviales han incrementado su uso para la interpretación paleoclimática, paleontológica y paleoecológica así como para las reconstrucciones paleoambientales.

Existen pocos estudios que se han enfocado en conocer la relación entre los depósitos aluviales y el desarrollo de los paleosuelos (Kraus y Aslan, 1993). Es importante resaltar este hecho ya que hay pocos estudios que tratan de explicar las características del hábitat donde caminaron los distintos vertebrados pleistocénicos en México (por ejemplo, Pérez Crespo, 2013, 2015, 2016).

No todos los registros paleoclimáticos son indicadores sensibles a cambios ambientales abruptos. Los diferentes proxies tienen diferentes niveles de inercia con

respecto al clima y esto no se responde con una mejor datación sino bajo el entendimiento del tipo de proxie utilizado así como la continuidad de su registro (Bradley, 1999). Es por esto que el uso y correcta comprensión de distintos proxies permite una reconstrucción paleoambiental más certera.

JUSTIFICACIÓN

México en la actualidad es un país megadiverso y se presume que debió ser más diverso en el pasado. Pocos estudios se han centrado en conocer los paleoambientes ocupados por las antiguas faunas, sus relaciones ecológicas y los cambios ocurridos desde el Pleistoceno tardío a la actualidad.

En México, la mayoría de los hallazgos de vertebrados fósiles son aislados, sin controles estratigráficos ni radiométricos. En muy pocas localidades con listados faunísticos se han realizado otro tipo de estudios (sedimentarios, paleosuelos) por lo que se conoce poco de la relación de la fauna a los ecosistemas que habitaron.

El estado de Puebla presenta el registro de vertebrados fósiles terrestres, particularmente mamíferos, más amplio que se conoce para el país. Sin embargo, poco se ha avanzado en conocer los escenarios en los cuales habitó dicha fauna. Los pocos acercamientos que se han realizado para poder cumplir este objetivo han sido a través de las asociaciones bióticas comparándolas contra sus análogos actuales y en el caso de la fauna extinta, basándose en los estudios realizados en otras partes del mundo, particularmente Estados Unidos. El problema de estos dos acercamientos para reconstruir las áreas de estudio radica en que:

- 1) las condiciones ambientales que debieron reinar en Estados Unidos durante el Pleistoceno tardío debieron de ser muy diferentes a las de México debido a su posición geográfica, particularmente si se compara con el sur del estado de Puebla;
- 2) que se ha mencionado que el tipo de asociaciones bióticas que estuvieron presentes durante el Pleistoceno no tienen análogos actuales y por eso se les conoce como no-análogos, disarmónicas o de incompatibilidad ecológica
- 3) que las asociaciones bióticas pueden ser producto del transporte.

La ventaja del uso de los paleosuelos y todos los constituyentes de su memoria edáfica radica en que se forman *in situ* dando claras indicaciones de cómo fueron las condiciones locales.

HIPÓTESIS

Los sistemas aluviales son sensibles al cambio ambiental por lo que dejan evidencias de esos cambios en sus registros. Se asume que las pedosecuencias de Santa Cruz Nuevo y Axamilpa, al no tener evidencias de tectónica activa durante el Pleistoceno, indicarán los cambios ambientales experimentados durante este periodo.

Se espera que se observen una serie de oscilaciones climáticas ya que es una característica del Pleistoceno tardío a nivel global. Estas oscilaciones climáticas, que tienen registro en el núcleo de hielo de Groenlandia, han sido detectadas en varias partes del mundo. Por lo anterior, las secuencias aquí estudiadas deberán reflejar estas oscilaciones climáticas, lo que permitirá correlacionarlas con otras cuencas cercanas y patrones globales.

OBJETIVOS

Objetivo central:

- Determinar los paisajes presentes en el estado de Puebla durante el Pleistoceno tardío a través del estudio de los paleosuelos y su contenido fósil dentro de dos secuencias edafogénicas aluviales, Santa Cruz Nuevo y Axamilpa.

Objetivos particulares:

- Analizar e interpretar los elementos de la memoria edáfica. Entre estos elementos se incluyen los rasgos macro y micromorfológicos, los fitolitos y la susceptibilidad magnética. El análisis micromorfológico en particular tendrá un papel preponderante para la reconstrucción del ambiente.
- Determinar los valores de isótopos estables del carbón en materia orgánica presente en suelo y en dientes de vertebrados pleistocénicos obtenidos de ambas localidades.
- Analizar el registro fósil de ambas secuencias para correlacionar la memoria edáfica con el registro fósil registrado en trabajos previos en ambas zonas de estudio.
- Comparar los modelos ambientales aquí generados con patrones climáticos nacionales e internacionales.

Resultados

En los tres artículos publicados, resultado de este trabajo de investigación, se interpretaron los paleoambientes presentes en ambas secuencias, Santa Cruz Nuevo y Axamilpa a través del uso de diferentes proxies como fueron los procesos pedogénicos dominantes, los isótopos estables de carbono, los isótopos de radiocarbono (^{14}C), fósiles y fitolitos.

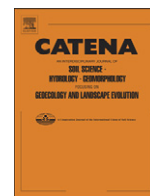
Los artículos son:

Tovar, R.E., Sedov, S., Montellano-Ballesteros, M., Solleiro, E., Benammi, M., 2014.

Paleosols, bones, phytoliths, and $\delta^{13}\text{C}$ signatures of humus and teeth in the alluvial sequence of Axamilpa, Puebla: Inferences for landscape evolution and megafauna paleoecology during MIS 3–2 in Southern Mexico, *Catena*, 112, 25–37.

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Paleosols, bones, phytoliths, and $\delta^{13}\text{C}$ signatures of humus and teeth in the alluvial sequence of Axamilpa, Puebla: Inferences for landscape evolution and megafauna paleoecology during MIS 3–2 in Southern Mexico

Rosa E. Tovar ^{a,*}, Sergey Sedov ^b, Marisol Montellano-Ballesteros ^b, Elizabeth Solleiro ^b, Mouloud Benammi ^c

^a Posgrado en Ciencias de la Tierra, Instituto de Geología, UNAM, Ciudad Universitaria s/n, Delegación Coyoacán, México, 04510, México

^b Instituto de Geología, UNAM, Ciudad Universitaria s/n, Delegación Coyoacán, México, 04510, Mexico

^c IPHEP, UMR-CNRS 7262, Université de Poitiers Bâtiment 35, 40 av. Recteur Pineau, F86022 Poitiers Cedex, France

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ABSTRACT

Alluvial paleosol–sedimentary sequences containing animal fossils, and paleobotanical and paleopedological archives have a potential for reconstructing Quaternary paleoenvironments in Southern Mexico and for understanding the paleoecology of Pleistocene megafauna. In the section of Axamilpa river four pedostratigraphic units were recognized. The lower Gleyic and Vertic pedological Units are at the end of marine isotopic stage (MIS) 3 while the upper Humic and (most probably) Calcic Units correspond to MIS 2 according to the radiocarbon dates of humus. The micromorphological analysis indicates an incipient development and syn-sedimentary character of paleopedogenesis in the periodically water-saturated environment (indicated by redoximorphic features, hydrogenic carbonates and low values of magnetic susceptibility in most strata). The $\delta^{13}\text{C}$ values of the paleosol humus range from -22.6 to -24.7 , indicating a C3 vegetation, whereas in the modern soil it is higher (-15.2) pointing to an abundance of the C4 and CAM plants. The $\delta^{13}\text{C}$ signature of the vegetation inferred from the teeth enamel of the fossil fauna appeared to be less negative than that of humus from corresponding paleosols. The alimentary preferences of the paleofauna which fed on grasses with high proportion of C4 plants explain this difference. The phytolith analysis shows dominance in conifer forms, followed by C4 and C3 grasses. The content of conifer phytoliths is progressively reduced towards the top of the sequence. We interpret the Late Pleistocene landscape of this area as a heterogeneous forest–grassland landscape with the forest shrinking through time and the grass areas increasing. Swampy floodplain meadows (inferred from paleopedological results) could provide a habitat for grassy vegetation. Both isotope and phytolith records demonstrate a contrasting difference between Pleistocene and recent vegetation dominated by xerophytic shrubs and succulents. This vegetation change could play important role in the extinction of Pleistocene megafauna.

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1. Introduction

The paleoecology of Mexico during the Late Pleistocene has recently drawn increasing interest. Being complex and affected by different factors its climatic system responded prone to the global climate changes of the last glacial–interglacial cycle. The paleoenvironmental reconstructions have been based mostly on the proxies extracted from the lacustrine sediment cores: sedimentological and micropaleontological data (e.g. Bradbury, 1971; Caballero and Ortega, 1998) and pollen analysis (e.g. Lozano-García and Xelhuanzi, 1997) together with the analysis of geoforms and sediments related to the glaciations of the highest mountains (Vázquez-Selem and Heine, 2004). These proxies provide a good temporal resolution, allowing through their integration, to trace the main paleoecological trends of the country and correlate them with the

global climate fluctuations (Caballero et al., 2010). However their spatial resolution is low just giving a regional view of landscapes. The geographical distribution of the lacustrine and glaciological records is extremely non-uniform: whereas Central Mexican Highlands are densely populated with study sites, the tropical south is still poorly documented. These aspects hamper the understanding of the geographical variability of the Quaternary landscape evolution in Mexico.

The insight of the Pleistocene landscape variability is especially important for the understanding of how the paleoenvironmental factors influenced present and past biodiversity in Mexico.

Nowadays Mexico is considered a megadiverse country, taking up the fourth position in biodiversity of the world. This position is given because of the great number of species but also because the abundant endemisms, ecosystems and genetic variability in some taxa (Espinosa et al., 2008). During the Pleistocene, the biota was also rich and diverse in North America; Martin (2005) postulated that the megaherbivore assemblage was richer than today, even richer than the present-day African fauna. Most of this vast and diverse fauna was lost at the end of

* Corresponding author. Tel.: +52 55 562242 80x219.

E-mail address: rosae_tovar@yahoo.com.mx (R.E. Tovar).

the Pleistocene in the course of a large-scale extinction event. The causes are still disputed (Koch and Barnosky, 2006).

Many documents of the Mexican Pleistocene fauna had been published (e.g. Arroyo-Cabrales et al., 2008; Corona-M, 2002; Ferrusquía-Villafranca et al., 2010) most of them, especially the earlier ones, being focused on the taxonomic identification. Much less is known about its paleoecology: the particular habitats of large mammals in the complex mosaic of Mexican Pleistocene paleoecosystems are still unknown. The other way around, the potential of vertebrate fossil materials to generate valuable paleoecological proxies at the regional scale has been underexplored. Only recently the first data on the stable carbon isotope composition of teeth from some Mexican Pleistocene mammals for paleovegetation reconstruction were published (Pérez-Crespo et al., 2009). More paleoenvironmental inferences could be obtained when the fossils are interpreted together with other proxies extracted from their geological setting. The study of the isotopic composition of mollusk shells in the famous Late Pleistocene paleontological and archeological site of Valsequillo/Puebla by Stevens et al. (2012) and combined paleontological, petrographic and palynological research in the Gomphoteriidae locality in Michoacán by Robles-Camacho et al. (2010) are promising examples of such approach.

We believe that the multidisciplinary analysis of the vertebrate fossil record together with various proxies from its geological context could provide rich and reliable information about past environments. Alluvial sedimentary sequences present attractive possibilities for such research. They often provide conditions for incorporation and preservation of paleontological remains – so that a large proportion of the known sites of the Pleistocene megafauna are associated with alluvial geosystems. At the same time they contain a set of associated paleoenvironmental proxies (paleopedological, sedimentological, paleobotanical) which are independent from each other but complementary increasing the reliability of interpretation.

In Mexico the Quaternary alluvial soil–sedimentary sequences have been already used for paleoecological reconstruction; most works are related to the Holocene dynamics, related to the human occupation history (Borejsza and Frederick, 2010; Butzer et al., 2008; Vita-Finzi, 1975). Few studies of the Pleistocene profiles were carried out in the Central and Northern parts of the country (Nordt, 2003; Solís-Castillo et al., 2012).

Alluvial sequences are well preserved in Southern Mexico which has fewer studies about Pleistocene environments although possessing a rich paleontological record (Ferrusquía-Villafranca et al., 2010). The goal of this work is to reconstruct the past environmental conditions of the locality named Axamilpa, Puebla, through the study of three proxies: paleosols, paleobotanical records (stable carbon isotopes and phytoliths) and mammalian fossil remains incorporated in an alluvial soil–sedimentary sequence.

We paid special attention to the paleosols which through their pedogenetic characteristics provide information about the local environmental conditions with high spatial resolution (Targulian and Goryachkin, 2004). In addition to the paleopedological record, the paleobotanical indicators from phytoliths and humus stable carbon isotope composition contained in the same paleosol strata were used.

2. Study area: ecological and geological setting, paleontological findings

The study area is located close to the town of Tepexi de Rodríguez, in the state of Puebla at 18°36'49" N, 97°54'45" W (Fig. 1); it corresponds to the eastern part of the Río Balsas Depression, known as the high Balsas. The basin is delimited by two morphotectonic provinces, to the north the Transmexican Volcanic Belt and to the south by Sierra Madre del Sur, and the Mountain System of the North of Oaxaca subprovince to the east (Fernández-Nava et al., 1998).

The modern climate of the area corresponds to type B, dry climate, where the precipitation is less than 500 mm per year (Rzedowsky, 1978). Nevertheless, the plant diversity is high. According to Arredondo-Gutiérrez (2009) in the Northeast, there are large areas of *crassicaule* shrubland while to the north and south there is a tropical deciduous forest. In the southwest there are large areas with chaparrals; in the center-west, there are few areas with oak forest and mesquite grasslands. Palms are present in all area.

The basement of Tepexi de Rodríguez region is constituted by the Paleozoic metamorphic rocks of the Acatlán Complex. Discordantly, the Cretaceous limestone of the Tlayúa Formation is found. The latter is overlain by the Paleogene polymictic conglomerate, and the andesitic tuffs and travertines of the Coatzingo Formation of Oligocene–Miocene age. The studied alluvial paleosol–sedimentary sequence forms a high accumulative terrace partly filling older Axamilpa valley. This older valley cuts deeply into the pre-Quaternary rocks mentioned above. The present day river bed is deeply incised in this terrace body; only very narrow discontinuous Holocene floodplain is formed in its bottom.

Many paleontological studies have been done in the area, the most famous deal with the excellently preserved Cretaceous fishes of Tlayúa Formation; also, the plants of Oligocene age are well known. Less attention has been given to the Pleistocene outcrops. Torres-Martínez and Agenbroad (1991) mentioned the discovery of a fossil turtle assigned to Testudinidae, and mammals: mammoth *Mammuthus columbi*, gomphotere *Cuvieronious* sp., horse *Equus* sp., bison *Bison* sp., camelid *Paleolama* sp. and glyptodont *Glyptodon* sp. in the Axamilpa valley, where the Pleistocene faunal remains are related to the high terrace alluvial sequence mentioned above (Fig. 1). Castro-Azuara (1997) reported the presence of a glyptodont assigned to *Glyptotherium* cf. *G. cylindricum* in the Colina del Gliptodonte; while Montellano-Ballesteros (2002) recorded the presence of gomphotere *Cuvieronious tropicus*, horse *Equus* sp., mammoth *Mammuthus* sp., mylodontid edentate *Glossotherium* (*Paramylodon*) *harlani*, glyptodont remains and an indeterminate antilocaprid in Rancho Gerardo site, belonging to Axamilpa valley (Fig. 1).

Montellano-Ballesteros (2002) proposed the first stratigraphic scheme for Axamilpa, recognizing three units based on their sedimentological characteristics: basal dark-brown silty-sand; middle yellowish silt and sand with lenses of rounded and elongated cobbles; and upper dark-brown silt and sand with irregularly shaped calcite concretions. The equid and mammoth remains belonged to the upper unit and the gomphotere and edentate material were found in the middle unit. However no instrumental dating, laboratory analyses or more detailed morphological characterization of sedimentary strata were carried out at the earlier stage of research, which was mostly focused on paleontological findings.

3. Materials and methods

The studied section (18°36'49" N, 97°54'45" W) is near 22 m thick and is close to the Axamilpa river from which it takes the name. The morphological characterization of the different paleopedological units was done following Birkeland (1999).

The design of laboratory methods intended to provide data for the two main proxies of environmental history: paleopedological and paleobotanical. Paleopedological block included a set of paleosol physical (grain size determination, magnetic susceptibility) and chemical (determination of percentage of CaCO₃ and organic carbon) parameters indicative of pedogenesis. Organic carbon values give an estimate of humus accumulation, whereas carbonate content informs about carbonate redistribution in the buried soils. The determination of CaCO₃ content was quantitative and was obtained in the following way: to 5 g of sieved sample 1 ml of 1 M HCl was added and mixed. Then, we centrifuged the samples at 5000 rpm (revolutions per minute) during 5 min and repeated the treatment until the samples stop reacting with acid and the pH was below 5. The samples were washed with

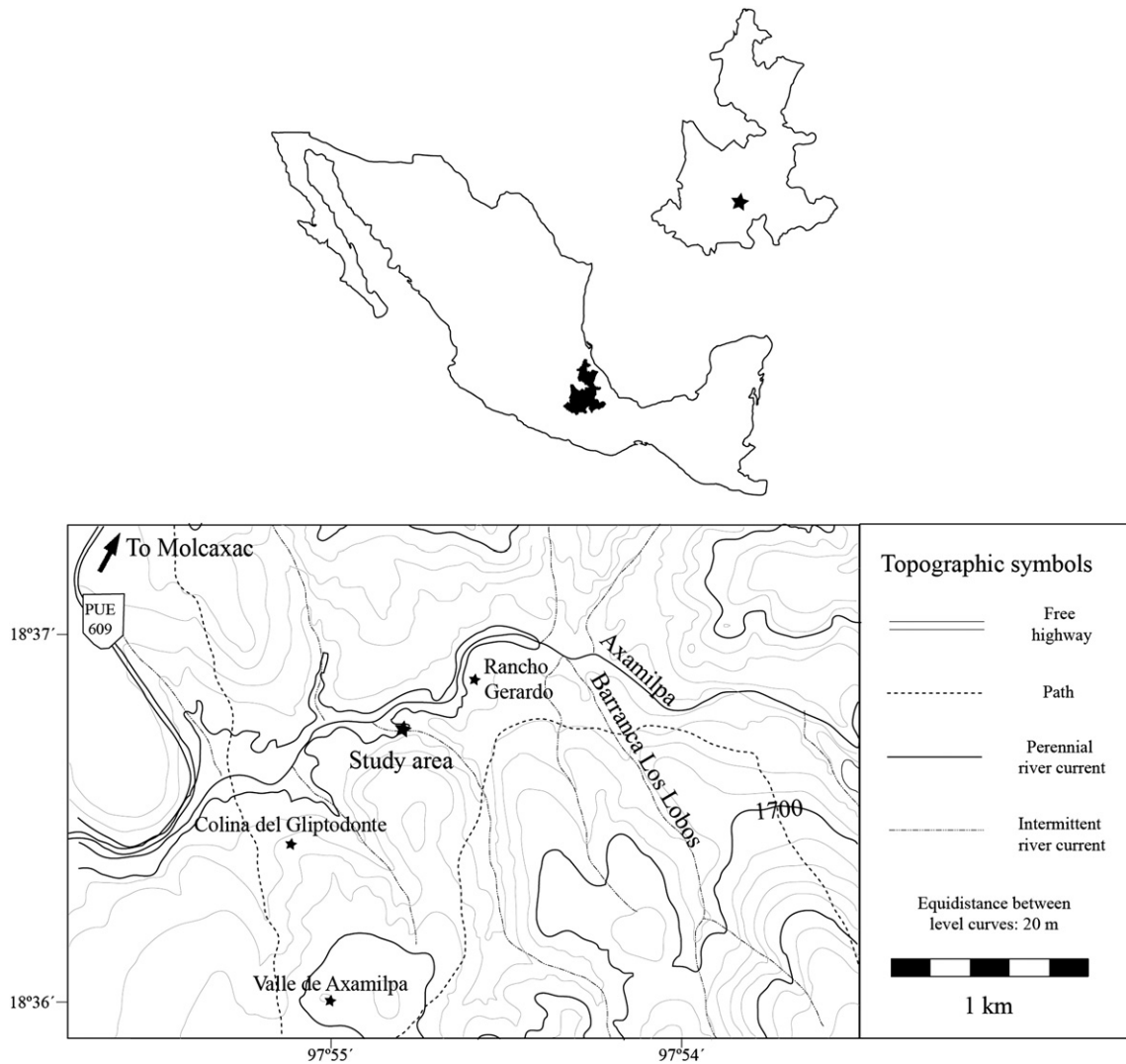


Fig. 1. Localization of the Axamilpa pedostratigraphic section marked with a big star. The other paleontological areas are indicated by small stars.

distilled water and centrifuged at 5000 rpm during 5 min; then dried at 40° during a week. Dried samples were weighed again and we interpreted the loss of weight as CaCO_3 content. One gram of these CaCO_3 free samples was analyzed for organic carbon determination using an Elemental Analyzer CHNS/O Perkin Elmer 2400 series II. To calculate the content of C_{org} in original material (containing carbonates) we used the next formula:

$$\%C_{\text{org}} \text{ of the original sample} = \%C_{\text{org}} \text{ of decalcified sample} \times [(100\% - \% \text{carbonate}) / 100].$$

Grain size distribution could help to evaluate weathering and pedogenic clay accumulation; however in the alluvial sequences it is controlled mostly by sedimentation processes, thus its importance for paleosol study consists in showing lithological discontinuities. For the grain size analysis we separated quantitatively the sand fractions (2–0.02 mm) by sieving, and estimated silt (0.02–0.002) and clay (0.002 mm) content by the hydrometer method (Gee and Or, 2002). Soil-forming processes strongly influence rock magnetic parameters, which is why magnetic susceptibility is frequently used in the paleosol-sedimentary sequences as a quantitative indicator of pedogenetic transformation. To determine the magnetic susceptibility, 1 cm^3 of every horizon was measured at two frequencies, low and high, with a Bartington MS2B sensor. Micromorphology is of special importance for detecting

pedogenetic processes in the poorly developed syn-sedimentary alluvial paleosols. Thin-sections (30 μm thick) were prepared from undisturbed soil samples impregnated at room temperature with the resin Cristal MC-40, studied under the petrographic microscope and described following the terminology of Bullock et al. (1985).

The paleobotanical proxy included the phytolith analysis and composition of stable carbon isotopes in the paleosol organic matter and paleofauna remains. The microscopic study of the phytolith assemblages is one of the main techniques for reconstructing paleovegetation (Piperno, 2006). It is especially appropriate for paleosols where organic plant fossils – pollen and macrorests are often poorly preserved whereas opaline phytoliths are relatively stable; besides phytoliths are less subjected to redeposition thus producing the paleovegetation signal with higher spatial precision (Golyeva, 2001). For the extraction of phytoliths we followed the method of Madella et al. (1998). The samples were mounted on the slides with glycerin and 200 forms of silica bodies were counted under a petrographic microscope. We preferred glycerin as mounting method because its refractive index is higher than that of opal but lower than that of all common silicates including volcanic glass. This helps to discriminate opaline particles from other minerals which contaminate the phytolith concentrates (for details see Sedov et al., 2003). However the results of the counting should be considered as semi-quantitative because of high variety of shapes and low number of particles in some of the diagnostic groups.

The analysis of stable carbon isotope composition (presented as $\delta^{13}\text{C}$) of the soil organic is increasingly utilized for paleobotanical reconstructions with further inferences for environmental history in a wide range of geographical and chronological contexts (e.g. Farquhar et al., 1989). The stable carbon isotopes from organic matter and tooth enamel provide information about the vegetation and their metabolic routes. C3 plants typically have mean carbon isotope ratios of -27% , C4 plants of -13% as do the drought-adapted succulent plants with obligate crassulacean acid metabolism (CAM) (Nunez et al., 2010). The analysis of $\delta^{13}\text{C}$ was successfully applied to late Quaternary paleosols in Mexico, where environmental changes often cause a dramatic shift in the proportion of plants with different types of photosynthesis, reflected in the carbon isotope signatures of paleosol humus (Lounejeva Baturina et al., 2006, 2007; Sedov et al., 2003). The samples used for $\delta^{13}\text{C}$ determination were pretreated with HCl 1 M in the same way as for evaluation of organic carbon and carbonate content. The routine combustion method (Sofer, 1980) was applied to prepare the specimens of CO_2 , and a triple collector mass spectrometer (Finnigan MAT250) to evaluate the $\delta^{13}\text{C}$ ratios of the soil organic matter (for details see Sedov et al., 2003).

The parallel study of phytoliths and stable carbon isotopes of humus from the same soil horizon gives an attractive chance to extract two methodologically independent paleovegetation proxies for a more complete and reliable reconstruction. This approach was already successfully applied to the Holocene soils of different environments (Alexandre et al., 1999; Kerns et al., 2001; McClung de Tapia and Adriano-Morán, 2012). Our research site provided opportunity to obtain an additional isotopic paleovegetation signal from the faunal remains having close stratigraphic relation to the paleosol horizons, based on the earlier paleontological investigations. Fossil vertebrate remains have been collected in various outcrops along the Axamilpa valley since 1991; the finds were reported by Torres-Martínez and Agenbroad (1991), Castro-Azuara (1997), and Montellano-Ballesteros (2002). The fossil material analyzed in this work were recovered from the middle and upper layers mentioned in Section 2. From the middle section, mastodon and edentate material was collected while remains of *Equus* sp., *Mammuthus* cf. *M. columbi* and *Glyptotherium* were collected in the upper lithological unit. In 2010 a joint field session was carried out to link all paleontological materials to the newly developed pedostratigraphic scheme.

For isotopic analyses we used teeth enamel of *Equus* sp. and *Cuvieronius tropicus* both from the upper and basal parts of the Calcic Unit and analyzed them in the Laboratorio Universitario de Geoquímica Isotópica (LUGIS) at UNAM. The method for preparing the enamel samples for stable isotopic composition analyses was similar to that described by Cerling et al. (1997). The tooth enamel was separated from dentine, then was crushed using an agate pestle and mortar, and sieved with a 125 μm mesh. Organic matter was removed with hydrogen peroxide (10 ml H_2O_2 30%, reaction time ~ 2 h). Next, the sample was centrifuged and washed three times with distilled water, a calcium acetate solution–acetic acid buffer (CaCH_3CO_2 – CH_3COOH 1 M, pH = 4.75, during ~ 9 h) – was used to strip diagenetic and adsorbed exogenous carbonates. The solution was then centrifuged and rinsed with distilled water. Finally, ethanol is added to the sample and evaporated at 90 °C overnight. The mass spectrometry measurements were done using a Delta Plus XL Continuous Flow Isotope Ratio Mass Spectrometer Thermoquest Finnigan equipped with Gas Bench II. To compare between the $\delta^{13}\text{C}$ values of the soil organic matter and the fossil teeth, we assumed an isotope enrichment of $\delta^{13}\text{C}$ of 14.1 that was consider for large ruminant mammals and their diet (Cerling and Harris, 1999).

The profile chronology was based on the radiocarbon dates from paleosol organic matter from the horizons. For this project, four samples from paleosol humus horizons and one charcoal sample were sent for radiocarbon dating. The samples were taken deep enough to be isolated from the effects of recent pedogenesis and free of modern roots. Samples were processed in the Beta Analytics laboratory and AMS dated.

The calibrate dates were obtained through <http://www.calpal-online.de/index.html>. We did not utilize pedogenic carbonates neither for stable carbon isotope studies nor for radiocarbon dating because primary carbonates (derived from the Cretaceous limestone) are abundant and the probability of their presence in the calcitic pedofeatures is very high.

Sampling strategies varied for different utilized methods. For grain size, organic carbon and carbonates bulk samples were taken from the paleosol genetic horizons along the whole section. Much denser equidistant sampling – every 10 cm – was carried out for rock magnetic studies. Undisturbed samples were taken from one paleosol profile of each morphological unit for preparation of thin sections. Only selected humus (Ah) horizons where highest concentration of soil organic matter and plant microfossils was expected, were sampled for the phytolith analysis, stable carbon isotope composition and radiocarbon dating. The position of the sampling localities at the pedostratigraphic scheme in marked in Fig. 2.

Finally, the obtained results and their paleoecological interpretation were integrated with the paleontological data from the locality and further compared with the available regional records of the Late Pleistocene environmental history.

4. Results

4.1. Pedostratigraphy, soil morphology and dating of the section

Axamilpa section has a total thickness of around 22 m and presents four major units discriminated on the base of their morphological features of their paleosols: Gleyic, Vertic, Calcic and Humic Units (Fig. 2).

4.1.1. Modern soil (0–149 cm)

The modern soil has a dark gray Ah horizon, 35 cm-thick with a granular structure and sandy loam texture. The AC horizon is lighter with more proportion of sand and the aggregates are unstable. The C horizon presents many clasts of Mesozoic limestone from the Tlayúa Formation. According to the World Reference Base (WRB) for Soil Resources 2006, it is classified as a Calcaric Phaeozem.

Modern soil is separated from the underlying paleosol unit by alluvial sediments 189 cm thick. They have sandy–gravelly composition, coarse lamination and differ greatly from much finer deposits below.

4.1.2. Humic Unit (338–630 cm)

This Unit includes three buried soils with dark gray-brown humic Ah horizons with predominantly blocky structure. The upper paleosol has thicker and more differentiated humus layer with a second Ah horizon (2A2) characterized by granular structure. The second soil has gleyed horizon 3Bg characterized by yellow patches of iron oxides.

4.1.3. Calcic Unit (630–1174 cm)

Two paleosols with strongly developed calcic horizons (which form notorious erosional steps within the exposure) comprise the specific feature of the Calcic Unit. The upper paleosol (5A–5ABk–5Bk1–5Bk2) has abundant hard carbonate concretions in the Bk horizons. In the lower paleosols (6A5sk–6AB–6Bg–6Bkm–6Bk) more advanced cementation with the secondary carbonates produced a hardened petrocalcic horizon (6Bkm). The lower horizon 6Bk has many elongated carbonate concretions with predominant sub-horizontal orientation. Both paleosol profiles have gray blocky silty–clayey humus horizons, the lower one has slicken-sides.

4.1.4. Vertic Unit (1174–2073 cm)

This most extensive Unit includes 10 paleosols (7–16) all demonstrating well developed vertic features. The dominant characteristic slicken-sides and angular blocky structure with wedge-shaped blocks, the texture is clayey. Concerning profile horization, many soils of this Unit are poorly developed with only an Ah and C horizons. The dominant dry color is yellowish gray (2.5 Y 5/1) while the wet color is dark

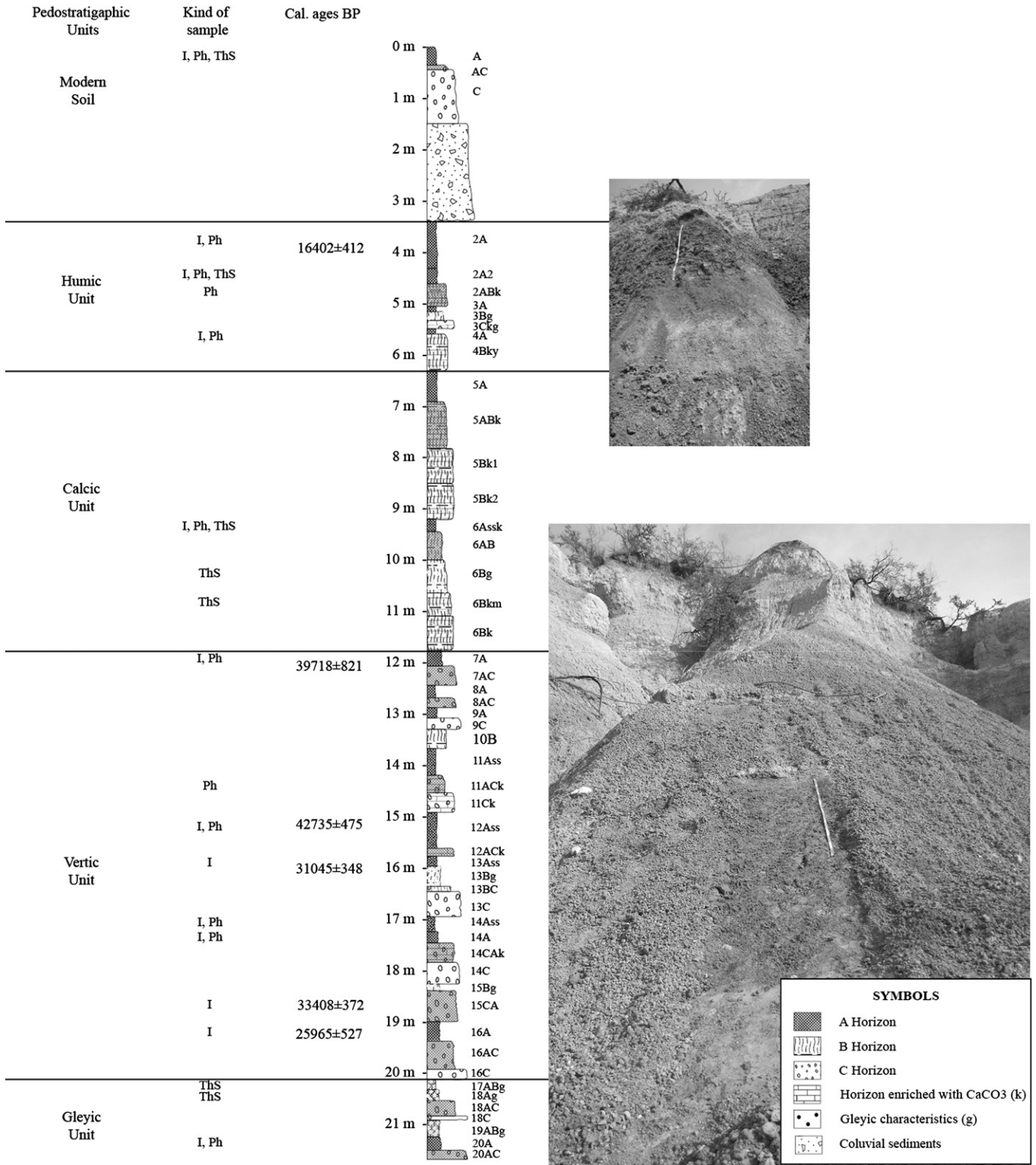


Fig. 2. The Axamilpa sequence with photos of different profiles, calibrated dates according to <http://www.calpal-online.de/index.html> and it is marked the kind of samples from the different horizons. I = Stable carbon isotopes. Ph = Phytoliths. ThS = Thin section.

grayish yellow (2.5Y 5/2). In the oldest soils (12 to 16) there are many pebbles in the horizons and in some occasions they are aligned (14C).

4.1.5. Gleyic Unit (2073–2228 cm)

This Unit includes four soils (17–20) poorly developed with silty-clay texture, dispersed pebbles of different sizes, and mottled

color pattern of yellow patches. This pigmentation typical for gleyzation gave the name to the Unit. In the paleosols 18Ag and 20A, the structure of the Ah horizon is composed of small blocks, in the 18 it shows vertic features as hard blocky aggregates and slicken-sides; however the proportion of silt is higher and the dry color is yellowish gray (2.5Y 6/1) and wet color is dark grayish yellow (2.5 Y 5/2) with yellow patches.

Table 1
Radiocarbon and calibrated ages of different horizons in the Axamilpa sequence.

Horizon, depth	Dated material	Radiocarbon age 14C yr BP	Calibrated age, cal yr BP	Laboratory code
15CA	Charcoal	28,900 ± 220	33408 ± 372	(Beta-261618)
13Ass	Humus	26,140 ± 170	31045 ± 348	(Beta-277567)
12Ass	Humus	38,310 ± 320	42735 ± 475	(Beta-300439)
7A	Humus	34,350 ± 270	39718 ± 821	(Beta-300438)
2A	Humus	13,450 ± 60	16402 ± 412	(Beta-261620)

Gypsum roses are found throughout the sequence demonstrating no clear relation to specific paleosol or sedimentary strata. We consider this neoformation to be of diagenetic or “deep soil” origin (see Alexandrovskiy et al. 2013, this volume), precipitated from groundwater after the sequence was formed.

Radiocarbon dates from four samples were obtained from different positions in the Vertic Unit (Fig. 2) and gave ages between 43 and 31 cal. ka BP (Table 1). A clear inversion is observed within this part of the section: dates from the lower 15CA and 13Ass are younger than overlying 12Ass and 7A horizons. Within these two couples however the ages are consistent with the depth.

4.2. Micromorphology of paleosols and recent soil

All sections show a fine material dominated by micrite and clay whereas coarse material consists of quartz and some fresh tephra particles: plagioclase, pyroxene and effusive rocks. Also, some clasts correspond to limestone of Tlayúa Formation (Early to Late Albian age).

The Gleyic Unit (Fig. 3A–C) presents, on the microscopic scale, rather few redoximorphic features like ferruginous nodules and mottles (Fig. 3B) together with abundant and clear evidences of digestive biological activity: the biogenic channels (Fig. 3A), micro-areas with granular structure of excremental origin, and vegetation remains (Fig. 3C).

Unexpectedly the Vertic Unit (Fig. 3D–F) bear more characteristics of sediment than of a paleosol. A net of fissures, some of them with wedge-shaped joints (typical of Vertic cracking) produce angular blocky structure; however within the blocks sedimentary microlamination is preserved (Fig. 3D). The biotic content corresponds principally to diatoms and fragments of orientated valves of mollusks, dark particles of decomposed organic detritus are also present. When biogenic particles have elongated shape they are oriented mostly parallel to the microlamination (Fig. 3E). Also, there are circular organic concentrations with cell morphology that we interpret as remains of algae colonies. The A horizon of the Calcic Unit, as the Vertic Unit, presents frequent sedimentary features (Fig. 3G–I). The thin section shows a coarse microlamination (Fig. 3G); frequent elongated charcoal particles follow the orientation of laminae (Fig. 3H). As pedological feature we observed micritic hypocoatings (Fig. 3I) and few ferruginous mottles.

The Humic Unit (Fig. 3J–K) is a more developed paleosol where sedimentary microstructure is absent. A dense net of channels and voids produced by roots and mesofauna as well as granular excremental aggregates are observed (Fig. 3J); at the same time few ferruginous nodules and coatings are present. In some pores we found compact infillings of large gypsum crystals with irregular shape (Fig. 3K), also present in other paleosol units. The most developed coprogenic granular structure, strong pigmentation with humus (Fig. 3L) and some fresh

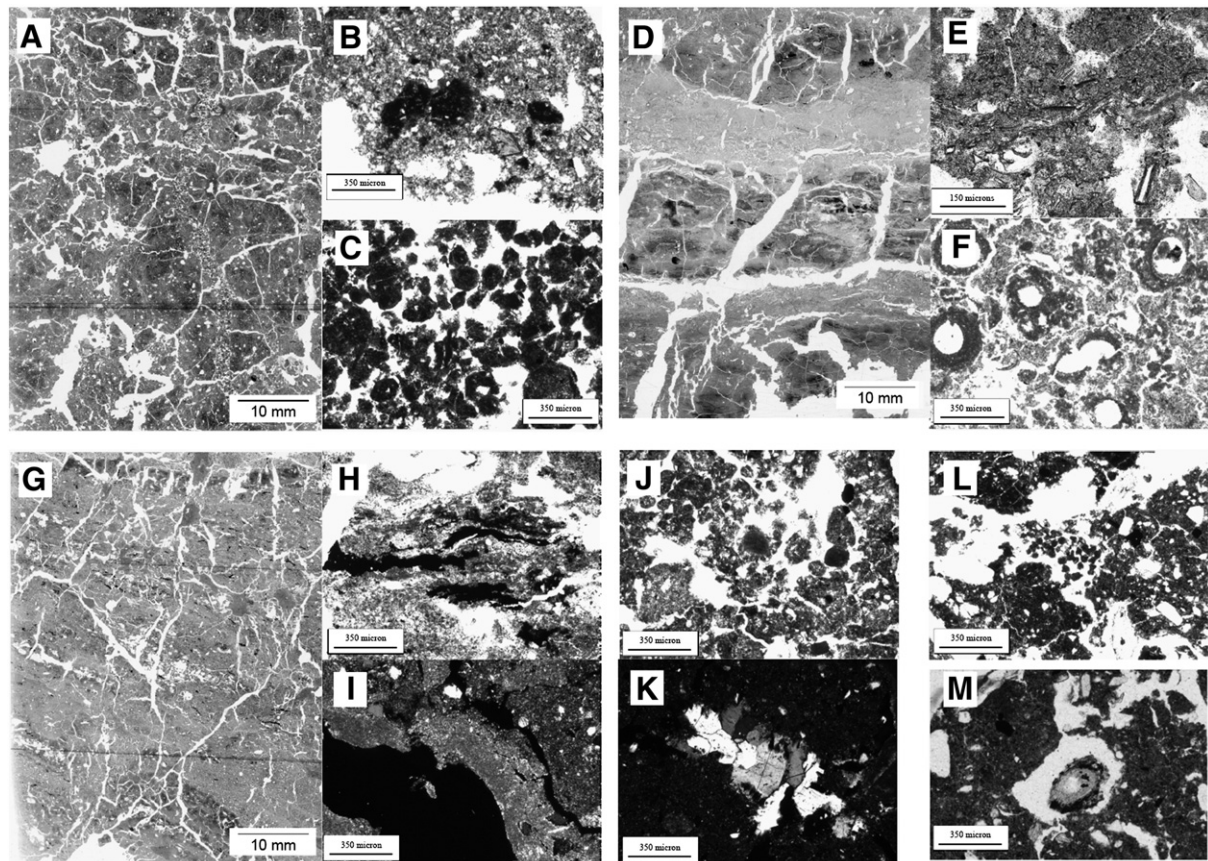


Fig. 3. Micromorphology of surface soil and buried paleosols of Axamilpa sequence. A, B and C (Gleyic Unit), D, E and F (Vertic Unit), G, H and I (Calcic Unit), J and K (Humic Unit), and L and M (Modern Soil). A. Macromorphological characteristics of a gleyic soil, see the biogenic channel in the center that crossed all the section. B. Oxide patches. C. Evidences of mesofauna. D. Macromorphological view of the vertic soil with sedimentary structure as fine laminations. E. Orientated diatoms. F. Circular growing cells interpreted as algae. G. Macromorphological view of a calcic soil with stratification. H. A close-up of the charcoal following the stratification. I. Micritic hypocoating. J. Evidences of mesofauna in the Humic Unit. K. Secondary gypsum. L. Evidences of mesofauna in the modern soil. M. A vegetation remain.

or partly decomposed plant fragments (Fig. 3M) were observed in the modern Phaeozem. In contrast to all paleosols, no redoximorphic ferruginous pedofeatures were found.

4.3. Physical and chemical characteristics of paleosols

Grain size distribution, carbonate content and organic carbon demonstrate rather irregular fluctuations along the section (Fig. 4). The grain size distribution shows a clear dominance of the finer particles, with a high content of clay, around 50–65% in most horizons; the highest values (70–80%) are observed in the thickest humus horizons 11Ass and 12Ass of the Vertic Unit. Only few strata demonstrate elevated (> 50%) concentrations of coarse fractions: sand in 13C and silt in 9C and 4A. The content of carbonates (CaCO₃) is around 20–30% with a higher proportion in the petrocalcic 6Bkm of the Calcic Unit (85%) and 12ACk of the Vertic Unit (64%) as well as in the modern soil (67%). The organic carbon content is low along all section (less than 0.5%) except in the modern soil (3.5%) and most developed Vertic humus horizon 11Ass (2.2%).

The magnetic susceptibility (χ) distribution is shown in Fig. 4. The highest values correspond to the modern soil, followed by the underlying colluvial sediments. In the paleosols, the highest values occur in the Humic Unit with clear enhancement in the buried Ah horizons (especially 2A). The lower values are recorded in the transition from the Gleyic to the Vertic Unit and in the middle and upper part of the Vertic Unit, including the thickest humus horizons 11Ass and 12Ass. At the same time at the bottom of the Gleyic Unit and in the lower part of the Vertic Unit some minor peaks are present. Comparing the Vertic Unit with the Calcic Unit, higher values are found in the latter; a sharp single maximum in the 6Bg horizon is associated with the concentration of charcoal and could have pyrogenic origin. Apart from these differences, the variations in the magnetic susceptibility in the middle and basal parts of the profile are moderate.

The results of the frequency-dependent susceptibility showed that in almost all Ah horizons there are evidences of superparamagnetic (SP) grains, however the highest values (>3%) are reached in the Humic Unit. SP minerals are fine secondary crystals produced by burning, bacterial activity and pedogenesis (Dearing, 1999).

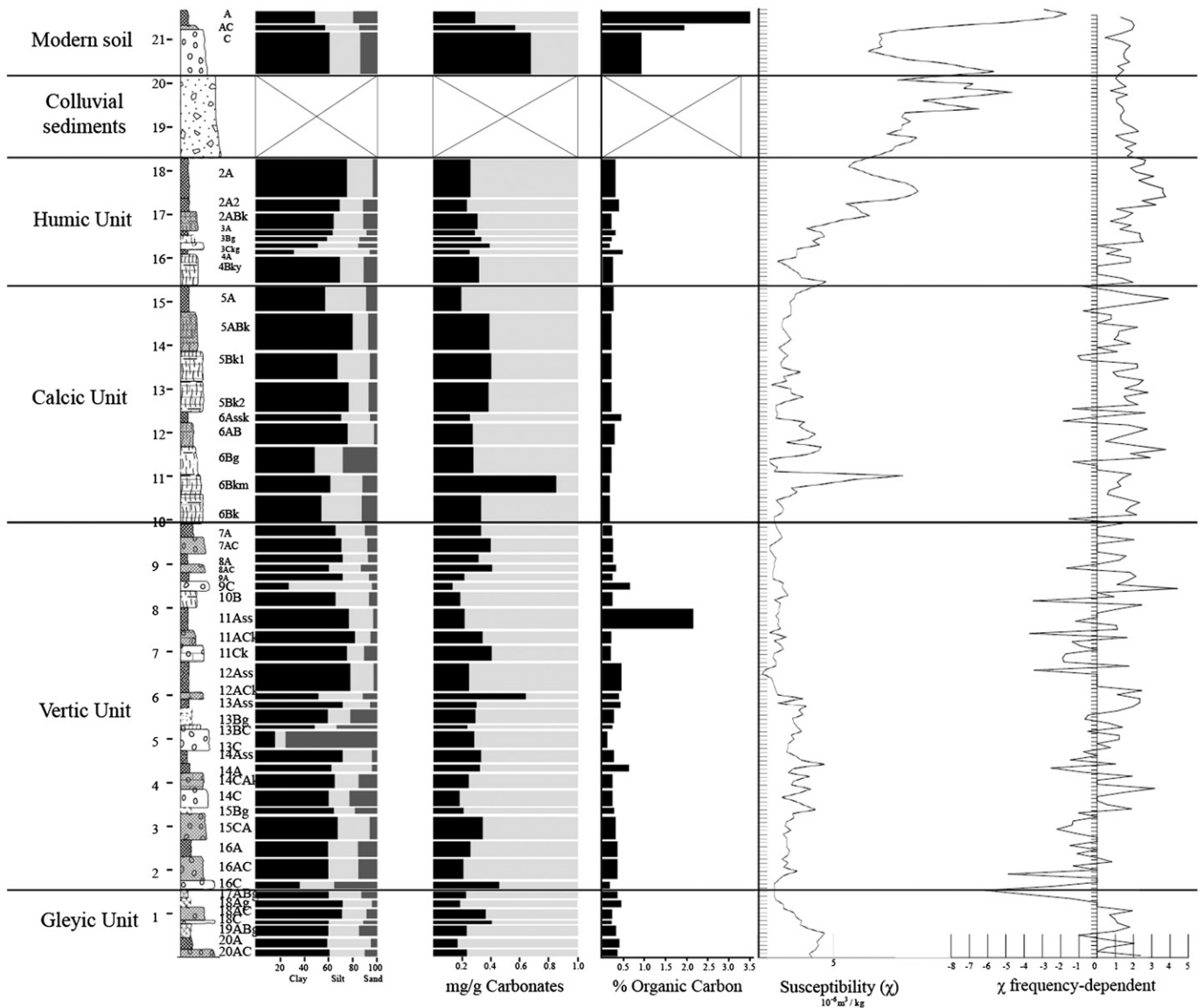


Fig. 4. Physical analyses of surface soil and buried paleosols. The first column shows the texture. See the big proportion of clay. Second column show the mg/g of inorganic carbonates and the third, the percentage of organic carbon. Next column corresponds to magnetic susceptibility, which is low all along except in the Humic Unit and the Modern Soil. The last column corresponds to frequency-dependent susceptibility. Values up to 2% indicate the presence of superparamagnetic minerals.

Table 2
Values of humus $\delta^{13}\text{C}$ signatures in the pedological units.

Horizon, Depth (cm)	Pedological Unit	$\delta^{13}\text{C}_{\text{VPDB}}$ (‰)
A (0–35)	Modern soil	–15.16
2A (338–431)	Humic unit	–23.91
2A2 (431–461)	Humic unit	–22.68
4A (548–558)	Humic unit	–23.48
6Assk (919–943)	Calcic unit	–23.54
7A (1174–1204)	Vertic Unit	–22.1
12Ass (1489–1559)	Vertic unit	–23.44
13Ass (1574–1638)	Vertic Unit	–21.9
14Ass (1707–1756)	Vertic unit	–24.71
14A (1756–1807)	Vertic unit	–23.10
16A (1960–1998)	Vertic Unit	–23.3
20A (2184–2210)	Gleyic unit	–24.60

Interestingly, the maximum in susceptibility in the modern soil as well as the high values in the underlying coarse alluvial sediments are not accompanied by high values in frequency-dependent susceptibility.

4.4. Vertebrate fossils: types, stratigraphy, preservation

From the lower part of the Calcic Unit, the middle section of Montellano-Ballesteros (2002), remains of mastodon and mylodontid edentate were recovered. According to her, the mastodon material, *Cuvieronius tropicus*, includes two lower jaws, upper tusks, and postcranial elements suggesting that at least two individuals are present: one very old and one juvenile. In the upper part of the Calcic Unit, the upper section of Montellano-Ballesteros (2002), isolated teeth and lower jaws of *Equus* sp., isolated teeth and postcranial remains of *Mammuthus* cf. *M. columbi* and scutes of *Glyptotherium* sp. were found. In addition, a carapace of *Glyptotherium* sp. was found outcropping in a correlative unit with the upper part of the Calcic Unit. Recently, all authors visited the study area and assigned a new level under the Gleyic Unit. From this level, many scutes of *Glyptotherium* sp. and some no identifiable elements of large bones have been recovered.

All these earlier and recent findings allowed the establishment of the following paleontological zones, correlative to the paleosol units:

- I. *Glyptotherium* sp. under the Gleyic Unit.
- II. *C. tropicus* and *Glossotherium* (*Paramylodon*) sp. from the lower Calcic Unit.
- III. *Equus* sp., *Mammuthus* cf. *M. columbi* and *Glyptotherium* sp. from the upper Calcic Unit.

4.5. Stable carbon isotope composition of humus and teeth

The values of $\delta^{13}\text{C}$ of humus in all paleosols are low ranging from –22.68 in the 2A2 horizon of upper Humic Unit to –24.6 (20A) 24.7 (14Ass) in the lower Vertic and Gleyic Units, that indicates C3 plants dominance. These signatures contrast with the high values in the recent soil (–15.16) corresponding to C4 and CAM vegetation (Table 2). Table 3 shows the values of $\delta^{13}\text{C}$ of *C. tropicus* and *Equus* sp. The $\delta^{13}\text{C}$ signature of the plant biomass on which these animals foddered, calculated using enrichment factor, is close to –17. As we see it does not coincide with the signatures of humus from the corresponding paleosols, being considerably heavier.

Table 3
 $\delta^{13}\text{C}$ of the teeth enamel of two genera of fossil mammals.

Taxon	Pedological Unit, Depth (cm)	$\delta^{13}\text{C}_{\text{VPDB}}$ (‰)	Enrichment factor of 14.1‰ ^a
<i>Cuvieronius tropicus</i>	Lower calcic unit (781–919)	–2.93	–17.03
<i>Equus</i> sp.	Upper calcic unit (919–1174)	–2.73	–16.83

^a According to Cerling and Harris, 1999.

4.6. Silica microfossils from the paleosols

Phytoliths, similar to stable carbon isotopes, were intended to be used to reconstruct paleovegetation. However in the course of micro-morphological observations as well as preliminary study of the phytolith concentrates we observed other biogenic opaline particles, belonging to aquatic organisms: diatoms and sponge spicules. We included these particles in the counts because their abundances provide additional valuable paleoenvironmental information (however we did not perform the complete diatom identification). The analysis of the abundances of different forms of biogenic silica particles (phytoliths, diatoms and sponge spicules) are shown in Table 4 and the most representative silica microfossils are shown in Fig. 5.

The Vertic Unit presents the most abundant and complete assemblage of silica forms. In the Gleyic, Calcic and Humic, phytoliths are fragmented and scarce, being less frequent in the Gleyic Unit. The modern soil does not present phytoliths neither other silica particle.

The most frequent silica bodies from the Gleyic soils correspond to cubic or gently elongated rectangular forms with regular pits on the surface (Fig. 5A) which were associated with conifers (Golyeva, 2011 personal communication), and are predominantly temperate plants. The elongate form (Fig. 5B) is second in abundance, it is diagnostic of the Gramineae, but is not specific for taxonomic identification on a lower level (Twiss et al., 1969). The circular, oblong and rondel (Fig. 5C left) forms characterize Pooideae (=Festucoideae), a C3 subfamily (Erra, 2010; Twiss, 1992).

The most abundant phytolith forms in the Vertic Unit are the saddles and elongate-forms. Other forms less abundant are echinate and bilobulate. The “squat” saddle-shapes (Fig. 5D) are present in the Chloridoideae subfamily (Piperno, 2006) belonging to the C4 grass type, which inhabits preferentially arid to semiarid environments (Twiss, 1992). Bilobulate forms (Fig. 5E), also named dumbbells,

Table 4
Relative abundances of silica microfossils of the different pedological units of the Axamilpa sequence.

	Gleyic Unit	Vertic Unit	Calcic Unit	Humic Unit
<i>C3 grasses</i>				
Circular		2.3%	1.0%	11.9%
Oblong	9.4%		8.0%	4.5%
Rondel		2.7%	4.0%	3.0%
Saddle	0.9%		1.5%	2.0%
Elongate	18.8%	14.4%	30.5%	26.7%
Sum	29.1%	19.4%	45%	48.1%
<i>Conifers</i>				
Cubic	22.2%	2.3%	14.0%	3.5%
Rectangular	21.4%			
Trapeziform short cell	0.9%	5.0%	2.0%	1.5%
Sum	44.5%	7.3%	16.0%	5.0%
<i>Other forms of C3</i>				
Point-shaped	15.4%		4.0%	3.0%
Globular echinate		7.7%		5.4%
Sum	15.4%	7.7%	4.0%	8.4%
<i>C4 grasses</i>				
Squat saddle	1.7%	23.9%	10.5%	11.9%
Dumbbell		6.8%	3.0%	4.0%
Polylobate	1.7%	1.8%	7.0%	3.5%
Doble saddle				0.5%
Sum	3.4%	32.5%	20.5%	19.9%
<i>Aquatic microfossils</i>				
Diatoms		24.8%	8.5%	14.4%
Sponge spicules		5.4%		2.0%
Sum		30.2%	8.5%	16.4%
Non-diagnostic forms	7.6%	2.9%	6.0%	2.2%
Total	100%	100%	100%	100%

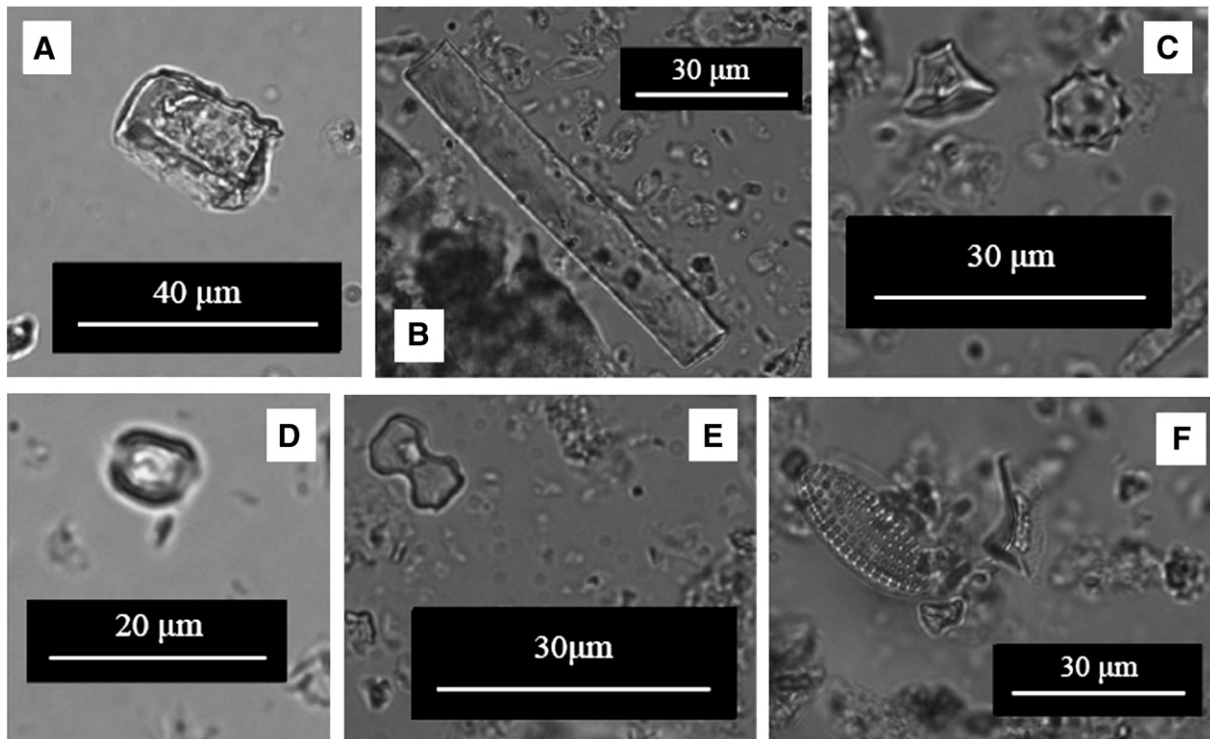


Fig. 5. The most representative forms of silica microfossils. A. Gently elongated rectangular form. B. Elongate form. C. Left, rondel; Right, echinate. D. Squat saddle. E. Bilobulate form. F. Diatom frustule.

and polilobulate forms are found in Panicoideae subfamily which also belong to the C4 vegetation (Erra, 2010).

The echinate forms (Fig. 5C right) have been assigned to Family Palmae (Arecaceae) which is predominantly tropical to subtropical family; however the genus *Brahea*, that is found close to the study area, grows on limestone-derived soils in semi-arid settings (Quero, 1994). Diatoms (24.8%) and sponge spicules (5.4%) show highest contents in the Vertic Unit indicating an aquatic environment (at least temporally).

In the Calcic Unit, the circular, oblong and rondel forms are assigned to Pooideae subfamily, the squat saddles – to Chloridoideae, the latter corresponds to C4 grasses. Also, we found a variation of the saddle-shape associated to Bambusoideae subfamily which is typical for tropical forest (Piperno, 2006). Aquatic microfossils are few.

Biogenic opaline particles of the Humic Unit include panicoid and chloridoid phytoliths, together with the forms assigned to palmas (echinate), conifers (elongated rectangular forms with regular pits on their surface) and bamboos (saddles). Diatoms and sponge spicules are also present although fewer than in Vertic Unit (14.4% and 2% respectively).

The trend along the sequence shows a decrease in the conifer forms towards the top; at the same time an increment in grass forms is observed.

5. Discussion

5.1. Paleopedological record: chronology and implications for local landscape history

The earlier paleontological findings allowed the establishment of the Pleistocene age of the Axamilpa sequence however without further detail. Our set of radiocarbon dates, all of them except one obtained from paleosol charcoal give an opportunity to precise the chronological scale of the sequence. We follow the widely accepted idea that the radiocarbon age of soil organic matter corresponds to

its mean residence time (MRT) in the soil system (Geyh et al., 1971). MRT is rather short in most temperate to tropical environments due to high decomposition rates (Trumbore, 2000; for Central Mexico – McClung de Tapia et al., 2005). Thus the 14C age of humus in the buried paleosols should provide an estimate for the “minimum age” of pedogenesis, close to the time of the burial (Matthews, 1985). The major problem of interpreting the radiocarbon datings consists in the inversion detected within the Vertic Unit: two upper dates from 7A and 12Ass horizons are significantly (6 to 10 ka) older than the ages of underlying 13Ass and 15CA horizons. Various factors affecting the isotope signal of the paleosol organic material are discussed, among them are: the contamination with recent components, in particular – root-derived (Geyh et al., 1971; Gocke et al., 2010); the input of eolian material especially in loessic sediments of arid environments (Liu et al., 2007); or the incorporation of older organic substances (Olsson, 1974). The inversion was detected in the deeply buried unit sealed from above by petrocalcic horizon, where large-scale recent root contamination is unlikely; also there are no evidences of large-scale eolian input in the studied sequence. On the other hand the buried humic horizons of the Vertic Unit have strong sedimentary features, as it will be clearly shown below. We believe that the dating inversion is due to redeposition of humus of older soil bodies incorporated into the sediment.

This explanation influences our interpretation of the whole set of dating: we conclude that they could provide only rough periodization of the sequence rather than precise chronology. Two “time windows” were determined: the lower part of the profile corresponds to the second half of the Marine Isotope Stage (MIS) 3, whereas the upper portion was formed during MIS 2. The limit between MIS 3 and MIS 2 is supposed to be within the uppermost Vertic and Calcic Units. Accumulation of the coarse alluvium which caps the sequence could take place during the Pleistocene–Holocene transition and corresponds to the quick aggradation event identified in the alluvial sequence in the neighboring Oaxaca after 10,300 yr. BP (Mueller et al., 2012). Increase of alluvial sedimentation during Pleistocene–

Holocene transition is recorded also in some valleys of Transmexican Volcanic Belt (Solleiro-Rebolledo et al., 2011).

Macromorphological observations in the field revealed buried soils as a notorious element of the sequence, with quite developed Humic, Calcic, Vertic and Gleyic horizons and features. However micromorphological investigations together with the paleosol physical and chemical data modified our earlier impressions about the grade of paleosol development, type of pedogenesis and its interaction with the sedimentation processes.

In the Gleyic Unit, the abundance of the biogenic pores and aggregates evidences a drained soil environment. Thus saturation with water and redoximorphic processes are responsible for gleyic features (mottled color pattern, ferruginous nodules) and were temporal. Maximum of magnetic susceptibility and presence of the pedogenic SP components also point to periodic soil aeration. Permanent water logging and anaerobic conditions usually destroy fine magnetic minerals and do not permit susceptibility enhancement (Grimley et al., 2004).

The micromorphological analysis of the Vertic Unit shows many sedimentary structures as orientation of the clasts and microlamination (Fig. 3D). Furthermore, the presence of mollusks, sponge spicules, diatoms and algal microstructures suggests a shallow lake or a marsh sedimentary environment. The vertic characteristics were developed later during the episodes of drying. However, the duration of vertic pedogenesis of these paleosols was short as far as it did not sweep away sedimentary features still observed in thin section. Formation of Vertisols on floodplain alluvial and deltaic clayey sediments is well known in recent Vertisols (Ahmad, 1983) and is controlled by flood intensity related to the particular geomorphic position (Fagan and Nanson, 2004). In tropical environment Vertisol pedogenesis on the alluvial clays could be rapid and related to the climatically induced drying (Pal et al., 2009). Buried Vertisols derived from muddy deposits are present in the late Quaternary terrestrial sedimentary sequences in tropics (Beuning et al., 1997).

Magnetic properties confirm this conclusion: in general the values of susceptibility are low. In the lower paleosols still some minor enhancement is visible associated with the presence of pedogenic SP particles. However in the upper part of this extensive Unit the magnetic susceptibility strongly decreases and reaches its minimum, no considerable enhancement is observed in the paleosol Ass horizons. This points to a weak effect of in situ soil formation and also agrees with the pedosediment accumulation in the anoxic swampy medium.

Conservation of sedimentary structures and weak overprint of post-depositional pedogenesis give a hint to explain the inversion of radiocarbon datings in the upper part of the Vertic Unit by incorporation of older redeposited organic materials.

Thin sections of the Calcic Unit as the Vertic Unit also demonstrates microlamination and particle orientation of the sedimentary origin (Fig. 3G). However, the texture of the sediment in this Unit is coarser and its biogenic content is different: charcoal and the freshwater mollusk shells are abundant. We suppose that this material was deposited by the fluvial processes of higher energy. As to pedogenic features we found evidences of abundant precipitation of secondary carbonates together with the features of weak redoximorphic processes and algal growth, indicative of temporal saturation with water. We assume that the major part of the carbonates in the Calcic Unit have hydrogenic origin and are precipitated from flood or groundwater. Within this assumption the concretionary partly cemented 5Bk and 6Bkm horizons are attributed to valley/channel calcretes related to groundwater precipitation (Alonzo-Zarza and Wright, 2010); this agrees with the spatial extension (restricted to the alluvial fill and disappearing towards watersheds) and morphology (absence of pedogenic horizonation, abrupt limits) of these horizons. Development of channel calcretes within the Late Pleistocene alluvial sequences in Jordan was recently interpreted as paleoclimatic signal of cooler conditions with restricted evaporation during the Last Glaciation (McLaren et al., 2012). As mentioned above, the available dating allows to suppose that the beginning of MIS 2 (marked by significant cooling on the global scale) is placed on the Calcic Unit containing calcretes.

The Humic Unit, by the other hand, presents a major accumulation of humus together with microscopic evidences of biogenic aggregation, porosity and no evidences of sedimentary structures. These characteristics suggest a more advanced pedogenesis of these soils formed far from the river influence where longer land surface stability was reached. The increment in the magnetic susceptibility and the highest values in the concentration of SP grains associated to pedogenetic activity support this idea. However, these paleosols also demonstrate redoximorphic pedofeatures indicative of the temporal water saturation. We correlate the paleosols of this Unit, according to their stratigraphic position, morphology and radiocarbon age to the “clayey organic-rich cumulic Ah horizons” formed during the final Pleistocene in the river valleys in Oaxaca (Mueller et al., 2012).

The modern soil demonstrates abundant evidences of biotic activity and humus accumulation that makes it somewhat similar to the buried paleosols of the Humic Unit. The difference consists in the complete absence of macro- and micromorphological evidences of redoximorphic processes. This means that these paleosols never experienced overmoisturing. Magnetic susceptibility reaches highest values however not due to pedogenic SP grains; that means this maximum has partial sedimentary origin. Similar maxima are observed in the underlying coarse alluvial strata.

We conclude that the pedogenesis of most paleosols is incipient. Mostly the rapid soil forming processes like gleyzation, humus accumulation and vertic structuring developed, their effects often being combined with the depositional features. In this case, the interpretation of the pedogenetic properties as a memory of past bioclimatic conditions is very limited. For example, Vertic soils are formed in arid or semi-arid zones (Fitzpatrick, 1984); however, when the vertic fracturing and aggregation is just a “camouflage” over sedimentary structures and components we can suppose their quick development after short-term drying of clayey sediments before the next sedimentation pulse. However the combination of pedogenic and sedimentary characteristics of paleosols says a lot about the local landscape conditions and surface processes in the river valley. Throughout the whole period of profile evolution soil development has syn-sedimentary character, the deposition type varying from slow fluvial to lacustrine and palustrine deposits. This supposes regular sheet flooding that could account also for periodic (but never permanent!) saturation with water and switch on redoximorphic processes. Furthermore we suppose that the secondary carbonate accumulation in the Calcic Unit resulted from hydrogenic precipitation rather than carbonate illuviation. This semi-hydromorphic syn-sedimentary floodplain pedogenesis finished with the deposition of coarse channel or levee alluvium and posterior dramatic quick incision of the river. The modern surface of the terrace and its corresponding soil has no influence of alluvial processes.

In order to understand better the paleoenvironmental setting of the Pleistocene fauna, paleosol record should be integrated with paleobotanical and fossil evidences.

5.2. Integration of the isotope and phytolith records for reconstructing Pleistocene environments

Stable carbon isotopes of the soil organic matter and phytolith assemblages are the blocks of soil memory which provide direct evidences about the composition of paleovegetation. These blocks are formed quite fast and are already present in the incipient soil profiles — that is important for the studied sequence dominated by poorly developed paleosols. This is quite different from the paleoecological interpretation of the block of pedogenetic–morphological and analytical characteristics which is carried out step-wise, via identification of the soil-forming processes. Many of the latter are quite slow (characteristic time 103–106 yr; Targulian and Krasilnikov, 2007) and cannot develop significantly in the dynamic alluvial geosystems. This makes the paleobotanical information to be of major importance for paleoenvironmental interpretation of the

alluvial paleosols. However, the indicators of paleovegetation have the following specific biases which we took into account:

- Isotopic composition of humus reflects the signature of total plant biomass incorporated in the soil body with only minor changes in the course of humification (Cerling et al., 1989; Farquhar et al., 1989) and thus is indicative of C3/C4/CAM proportions in the whole ancient flora.
- Phytolith assemblages are composed by the plants most efficient in generating silicified cells. Part of paleovegetation may not be reflected in the phytolith record simply because it does not produce the opaline bodies of specific shape (Golyeva, 2007).
- Taking into account that the paleosols are syn-sedimentary, part of humus and phytoliths could be redeposited thus both carbon isotopes and phytoliths provide a paleovegetation record of the whole river basin rather than a local signal only from the ancient floodplain.
- The isotopic signature of the fossil teeth enamel depends not only upon the ancient plant cover but also upon the alimental preferences of paleofauna.

The $\delta^{13}\text{C}$ isotopic values of organic matter in all paleosols range from -22.68 to -24.71% that clearly indicates that the paleoflora was dominated by C3 plants. As far as only minor variations are observed within the $\delta^{13}\text{C}$ curve we conclude that a C3 ecosystem prevailed throughout the second half of the Late Pleistocene, that could be woodland or forest as well as semihumid grasslands (Cerling et al., 1997). The contrasting difference of the $\delta^{13}\text{C}$ signature in the buried paleosols and modern soil should reflect a dramatic change of vegetation at the Pleistocene–Holocene transition. Very similar trend was recorded by Lounejeva-Baturina et al. (2006) in the Basin of Mexico where the $\delta^{13}\text{C}$ values also increase significantly in the Holocene soils compared to the Pleistocene paleosols – which allows to suggest a regional tendency. The phytolith record provides more details of the paleoflora composition. The most abundant forms correspond to grasses followed by conifers. This combination indicates mixed vegetation where forested areas were combined with grassland patches. Part of the grasslands could be represented by the moist wetland meadows in the floodplain which we could infer from the paleosol record.

Unexpectedly, C4 grasses (Families Chloridoideae and Panicoideae) appear to be an important part of the vegetation, particularly in the Vertic Unit (Table 4). We conclude that the C4 grasses were always present in the Pleistocene ecosystems however their contribution to the total biomass was minor and poorly recorded in the carbon isotope record.

We further propose that the absence of the phytoliths in the modern soil is also a significant botanical signal. As it was described above this soil shows a well developed complete profile with mature surface humus horizon thus one does not expect the loss of the phytolith pool due to soil erosion or degradation. Strong phytolith weathering is improbable taking into account semiarid climate and abundance of carbonates in the soil material. Radiocarbon dating of biogenic opal particles confirmed their persistence throughout the Holocene in the humus horizon of a surface prairie soil (Wilding, 1967); grass phytoliths are known to be preserved even in pre-Quaternary contexts (Strömberg, 2004). We conclude that the plant opaline microfossils are absent because the primary input is lacking: the main phytolith producers (namely conifers and especially Gramineae grasses) have been few in the modern vegetation. This difference from the paleosols, together with the shift of the stable carbon isotope signature, points to the dramatic change of vegetation from the Late Pleistocene to the modern ecosystems.

Variations of the phytolith composition along the profile allow further paleoecological inferences.

In the Gleyic Unit conifer forms that are less produced by plants than grass phytoliths dominates (Dinan and Rowlett, 1993). Therefore, the abundance of conifer phytoliths suggests that these plants dominated

the area providing closed forest vegetation that implies a humid, possibly cooler climate (Piperno, 2006).

The major peak of C4 grass phytoliths is found in the Vertic paleosols. This increase is accompanied by a decrement of C3 grasses and conifer forms. We associate this phytolith signal with the development of vertic features of paleosols and interpret them all together as an evidence of drier periods which took place towards the end of the MIS 3. However dry climate was not dominant, humid conditions prevailed, maintaining the aquatic syn-sedimentary pedogenesis on the floodplain, the dominance of C3 plants and presence of Palmae in the paleovegetation.

More prominent tendency is the progressive diminution of conifer forms and C4 grasses since the establishment of Vertic paleosols and the constant increase of C3 grasses. Concerning the interpretation of the carbon isotope signature we conclude that similar low $\delta^{13}\text{C}$ values in the lower Gleyic Unit were related to the contribution of the tree biomass whereas in the upper Humic Unit – to the herbaceous vegetation. These results suggest a certain evolution of the heterogeneous landscape with reduction in the forest area and the increment of grasslands since the end of MIS 3 until MIS 2.

Our paleoenvironmental inferences are congruent with other available regional records. The nearest one is located in the San Juan Raya region, around 50 km away of the study area. Canul-Montañez (2008) studied the fossil pollen association and concluded that since 25,000 to 9000 RCYBP the area was dominated by a *Pinus/Quercus* forest. This agrees with the general outline of both isotopic and phytolith proxies of Axamilpa. The results of both localities, Axamilpa and San Juan Raya, suggest that the south of Puebla, where nowadays is established the semi-arid landscape of the Tehuacan–Cuicatlan Biosphere Reserve, was more humid and cooler during Late Pleistocene than today.

The trend towards aridization and contrasting seasonal variations at the end of MIS3 and beginning of MIS2 (between 35,000 and 20,000 yr BP) was recently inferred from the isotope composition of the freshwater mollusk shells in Valsequillo, north of Puebla (Stevens et al., 2012). Correlating the records of Axamilpa and Valsequillo is especially important because the latter is also derived from the alluvial sediments containing Pleistocene megafauna and possibly – evidences of human presence (although still to be confirmed). The general trend towards the decrease of forest vegetation and spread of grasses approaching the Last Glacial Maximum was inferred from a number of palynological spectra obtained from the lacustrine sediments in the Central Mexican Highlands (e.g. Lozano-García et al., 2005; Ortega-Guerrero et al., 2000). Paleoclimatic implications of this change are unclear: being interpreted earlier as evidence of aridization, and recently it was reconsidered as the possible result of downward shift of altitudinal vegetation zones and spreading of the alpine meadows induced by cooling (Caballero et al., 2010).

The joint interpretation of the stable carbon isotope and phytolith records gives hint to an interpretation of the isotopic signature of animal fossils. The $\delta^{13}\text{C}$ values of enamel teeth found in the Calcic Unit, assuming an enrichment of ^{13}C of 14.1 (Cerling and Harris, 1999; Table 3), correspond to a mixed diet with a dominance of C4 plants. These values are in a seeming contradiction with the humus isotopic records.

We attribute these discrepancies to the alimentary preferences of paleofauna. Herbivores exert a big influence in the landscape disturbing it especially because their plant consumption is selective (Augustine and McNaughton, 1998). Horses are dominantly grazers and the Mexican populations had shown mixed diets (Bravo-Cuevas et al., 2011; Nunez et al., 2010; Pérez-Crespo et al., 2009). On the other hand, the proboscidean *Cuvieronius* also had been reported as a mixed feeder, apparently as an ecological strategy because its sympatric distribution with *Mammuthus columbi* (92% of C4 vegetation) and *Mammuthus americanus* (90% C3 vegetation; Webb et al., 2004). Thus we suppose that the animals – “owners” of the studied teeth

had a preference for grasses among which the proportion of C4 plants was relatively high — as demonstrated by the phytolith assemblages. Due to these preferences the C4 grass biomass could contribute much more to the isotope signature of teeth enamel than of paleosol humus. Reconstructing the paleoecological setting of the Pleistocene megafauna we conclude that the grassland component of the complex patchy vegetation was of primary importance for the large-sized grazers. The dramatic vegetation change after the end of Pleistocene marked with the shrink of the grass component could be an important factor of the megafauna extinction.

This study is an example of how the combination of different proxies from the same profile increases the reliability of paleoenvironmental reconstructions and how risky could be the paleoecological inferences based only on one proxy, without cross-check through correlation with other independent records.

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The alluvial sequence of Santa Cruz Nuevo, Mexico: Paleoecological interpretation of fossil vertebrates and pedosediments from marine isotope stage 3

Rosa E. Tovar^{1,*}, Sergey Sedov², Marisol Montellano-Ballesteros², and Elizabeth Solleiro²

¹ Posgrado en Ciencias de la Tierra, Instituto de Geología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Delegación Coyoacán, 04510 Cd. de México, Mexico.

² Instituto de Geología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Delegación Coyoacán, 04510 Cd. de México, Mexico.

*rosae.tovar@ciencias.unam.mx

ABSTRACT

The Pleistocene was climatically variable worldwide. In Mexico, climatic changes have been primarily studied in central and northern regions of the country, particularly in regard to marine isotope stage 2 (MIS 2). The paleoenvironments of the previous interglacial, MIS 3, remain less known, especially in the south. In the present work, the results for an alluvial pedosequence in Santa Cruz Nuevo, Puebla are presented; the large and small vertebrates recovered from this locality were used to reconstruct past paleoenvironments. However, it was found that the suite of fossil microvertebrates used here was more informative than that of the macrofossils because they are still extant, thus allowing insights into their ecology.

Radiocarbon dating of the pedosequence indicates it was formed during MIS 3, around 30,000 radiocarbon years before present. Four pedological units were recognized: stagnogleyic, carbonate, gley and humus. With the exception of the carbonate unit, fossils were retrieved from all pedological units. Paleosols varied between Fluvisols and Gleysols, neither of which is diagnostic of any particular climate. Nevertheless, they are both hydromorphic, a condition that could result from intermittent flooding.

At the base of the section, in the stagnogleyic unit, the presence of mammoth bones in conjunction with negative values of $\delta^{13}\text{C}$ (-23.3 ‰) in paleosols suggest the existence of grassland with a dominance of C3 grasses. The isotopic values are similar in the succeeding units (-23 to -22 ‰); however, the fossil association found in Santa Cruz Nuevo indicates the incorporation of shrubland faunas. It can thus be inferred that the plant composition in Santa Cruz Nuevo comprised C3 grasses and CAM metabolic succulents such as cacti and magueys. Hydrated CAM plants use the ribulose 1,5-biphosphate (RBP) carboxylase enzyme, which produces negative values comparable to those of C3 plants. The uppermost unit, the humus, has a similar fossil association, but in spite of this, the paleosol-based isotopic values suggest a vegetation mix, indicated by the presence of C4 plants such as grasses.

The comparison of our results with other records suggests that the end of MIS 3 was a dry phase which changed to humid, and in some

places cool conditions, during MIS 2. No MIS 2 record is preserved in the Santa Cruz Nuevo pedosequence. The comparison of the modern soil and climate with our pedosequence shows more humid conditions during MIS 3. Finally, and although the microvertebrate associations are similar to extant ones, the macrovertebrates also encompass extinct taxa.

Key words: microvertebrates; alluvial sequence; paleosols; marine isotope stage 3; Puebla; Mexico.

RESUMEN

El Pleistoceno fue un periodo de variados cambios climáticos. En México, los cambios climáticos han sido más estudiados en las porciones centro y norte del país, particularmente los de la etapa isotópica marina 2. Los paleoambientes del periodo glacial previo, la etapa isotópica marina 3, son menos conocidos, especialmente en la porción sur. En este trabajo presentamos los resultados para una pedosecuencia aluvial en Santa Cruz Nuevo, Puebla, donde se han encontrado fósiles de vertebrados, con una gran proporción de microvertebrados asociados a paleosuelos. Los fósiles fueron usados para reconstruir los paleoambientes, sin embargo, los microvertebrados fósiles fueron más útiles debido a que continúan presentes en el área y a través de sus análogos actuales podemos reconocer sus requerimientos ecológicos.

La datación por radiocarbono de la pedosecuencia indica que se formó durante la etapa isotópica marina 3, alrededor de los 30,000 años de radiocarbono antes del Presente. Se reconocieron cuatro unidades pedológicas: estagnogleica, carbonatada, gleyca y húmica. En todas se encontraron fósiles con excepción de la unidad carbonatada. Los paleosuelos varían entre Fluvisoles y Gleysols, los cuales no son diagnósticos para un clima en particular. Sin embargo, son indicativos de hidromorfismo que pudo ser resultado de inundaciones temporales.

Se usaron datos de $\delta^{13}\text{C}$ de paleosuelos y las asociaciones de microvertebrados como los registros más importantes para las reconstrucciones paleoambientales. En la base, en la unidad estagnogleyca, la presencia de huesos de mamut y los valores negativos de

$\delta^{13}\text{C}$ (-23.3‰) sugieren la existencia de un pastizal con dominancia de pastos C3. Los valores isotópicos son similares en las siguientes unidades (-23 a -22 ‰), sin embargo, la asociación fósil indica la incorporación de habitantes de matorrales. Con base en ambos registros, inferimos que las plantas correspondieron a pastos C3 y suculentas como los cactus y magueyes que tienen metabolismo CAM. Las plantas CAM, que sí disponen de agua, usan la ribulosa 1,5-bisfosfato carboxilasa dando valores negativos como lo hacen las plantas C3. La última unidad, la húmica, tiene una asociación fósil similar pero los valores isotópicos de los paleosuelos sugieren una mezcla en vegetación, indicativa de la incorporación de plantas C4 como los pastos C4.

La comparación de nuestros resultados con otros registros sugiere que el final de la MIS 3 fue seco y que cambió, durante la etapa isotópica marina 2, a condiciones húmedas y templadas en algunas zonas. En la pedosecuencia estudiada no encontramos registro de la etapa isotópica marina 2. La comparación del suelo moderno y clima con respecto a nuestra pedosecuencia muestra condiciones más húmedas durante la etapa isotópica marina 3 y a pesar de que las asociaciones de microvertebrados son similares a las actuales, existen algunos elementos que se extirparon y la megafauna se extinguió.

Palabras clave: microvertebrados; secuencia aluvial; paleosuelos; etapa isotópica marina 3; Puebla; México.

INTRODUCTION

Paleoecological interpretations, at least for the Phanerozoic and particularly for the Quaternary, are mainly based on the uniformitarianism and actualism principles. Uniformitarianism was proposed by James Hutton (1726–1797) and assumes that the geological processes that currently operate are the same that operated in the past. In other words, “the present is the key to the past”. Actualism includes the direct comparison of different sources of information provided from fossils, sediments and paleosols with modern analogs.

During the Pleistocene, there was a rich biotic diversity of mammals in different regions of the world (North and South America, Europe and Australia), and it has been suggested that this biodiversity was richer than at present (Semken *et al.*, 2010). However, the ecological requirements of macrovertebrates are not yet completely understood and paleoecological inferences from these fossils are still ambiguous and uncertain. On the other hand, microvertebrates, with their high reproductive rates and low extinction ratios, are ideal tools for paleoecological reconstructions. Furthermore, when small vertebrate remains are found along with megafauna, they ultimately contribute with valuable information on the paleoecology of the latter.

Although the use of fossil microvertebrates has many approaches in taxonomy, paleobiogeography, paleobiology and evolution (*e.g.*, Sankey and Baszio, 2008), their main application in archaeology and Pleistocene paleontology is in the reconstruction of paleoecosystems. Through an analogy of archaeological and fossil microvertebrate remains it is possible to make paleoecological inferences because, in the modern natural contexts of the same species, they represent the local fauna and have narrow ecological requirements (Stahl, 1996).

The paleoecological analyses of many late Pleistocene faunal communities have established combinations of species which are ecologically incompatible at present. These assemblages are known as disharmonic, non-analog, or intermingled faunal associations (Fay, 1988; Graham, 1986; Graham and Lundelius, 1989). Evidence of disharmonic associations are numerous worldwide (Markova *et al.*, 2002, 2010, Ceballos *et al.* 2010).

In this context, it can be said that microvertebrate fossil faunas are the key to the paleoecological reconstructions of disharmonic associations. In Mexico, fossil microvertebrates are found in caves (*e.g.*, Arroyo-Cabrales and Polaco, 2003), ancient lakes (*e.g.*, Álvarez and Hernández-Chávez, 1994), ancient springs (*e.g.*, Álvarez and Álvarez-Castañeda, 1991) and ancient rivers (*e.g.*, Van Devender *et al.*, 1985) during the Pleistocene.

Soils developed over floodplains preserve a good record of the environmental conditions, geomorphology and/or local conditions. In alluvial sequences, microvertebrates are mainly found in the terrace sediments accumulated in earlier floodplains. Macromorphological characteristics are one of the many clues soils register in their soil memory. Soil memory is the ability of the soil system to record the environmental phenomena through pedogenetic processes that act *in situ* (Targulian and Goryachkin, 2004). Other soil memory elements in alluvial soils are humus $\delta^{13}\text{C}$, which are remains of organisms or their biotic activity such as feces, channels, phytoliths and magnetic susceptibility.

The use of combined records of soil memory and fossil vertebrates helps to interpret the environmental conditions that prevailed in an area (*e.g.*, Solís-Castillo *et al.*, 2012; Tovar *et al.*, 2013, 2014). However, the recognition of disharmonic associations and the absence of knowledge on megafaunal habitats might be one of the reasons for a limited use of paleofaunas as paleoenvironmental indicators in Mexico. As a matter of fact, Mexican microvertebrate fossil remains are very little known and their use is restricted to taxonomic designation.

The goal of this article is to reconstruct the paleoenvironments of Santa Cruz Nuevo from the late Pleistocene to the present by studying macro and micro fossil vertebrates, paleosols and some elements of their soil memory.

STUDY AREA

The study area is located in the vicinity of the town of Santa Cruz Nuevo, southern Puebla, Mexico (Figure 1). Two different climatic settings are present in Santa Cruz Nuevo. The predominant climate is semi-warm subhumid with summer rains A(C)wO(w); the average annual temperature varies between 22 and 25 °C. The secondary climate, present in the northeast portion of the community, is subhumid temperate with summer rains C(w)O(W), and its average annual temperature varies between 17 and 19 °C. The vegetation is rosetophyll shrubland. A gallery forest borders the Acatlán river.

The Quaternary outcrops overlay the Mixteca terrain, which has been characterized by the Acatlán Complex. The Acatlán Complex comprises igneous and sedimentary rocks ranging from the Paleozoic to the Quaternary (Morán-Zenteno, 1994). The Santa Cruz Nuevo sediments belong to the latter.

In 2006, Tovar and Montellano reported the presence of 22 families, 24 genera and 11 species of fossil vertebrates in the study area.

MATERIAL AND METHODS

Four overlapping profiles (A-D) along the Acatlán river were described and measured. Six pedostratigraphic units were recognized on the basis of their macromorphological features and named according to their predominant pedological or sedimentological characteristics. The description of the soil features was achieved according to Birkeland (1999).

Bulk samples from every unit were taken for physical and chemical analyses, unaltered samples for thin sections, and samples presenting

organic matter from selected horizons for radiocarbon dating.

Thin-sections (30 µm) were prepared from undisturbed soil samples, impregnated with the resin Cristal MC-40 at room temperature, studied under a petrographic microscope and described according to Bullock *et al.* (1985).

Humus and charcoal samples were sent to Beta Analytic Inc. for age estimation through Accelerator Mass Spectrometry (AMS). All dates were reported in radiocarbon ages before present (¹⁴C ages BP) and in calibrated ages according to <www.calpal.de>. Stable carbon isotopes, reported as δ¹³C, were obtained from organic matter in paleosols and sent to Laboratorio Universitario de Geoquímica Isotópica (LUGIS), UNAM.

To establish particle-size distribution quantitatively, sand (2–0.02 mm) was divided in fractions by sieving, while silt (0.02–0.002 mm) and clay (< 0.002 mm) were separated through the hydrometer method (Gee and Or, 2002).

Fossil vertebrates have been collected from the Santa Cruz Nuevo locality since 2001. Microvertebrate remains were recovered by the screen-washing technique, and megafaunal remains were recovered by using gypsum splints or toilet tissue wraps. The fossils collected were assigned to a pedologic unit or layer. All fossil material was prepared in the Laboratorio de Paleontología, Instituto de Geología, UNAM, and ultimately deposited in the Colección Nacional de Paleontología, at the same institute.

RESULTS

Stratigraphy and soil characteristics

Two pedostratigraphic sections were analyzed and correlated through marker soils. Four pedostratigraphic units were recognized in the study area of Santa Cruz Nuevo, Puebla, Mexico, and were identified as stagnogleyic, carbonate, gley and humus (Figures 2 and

3). Among the different units, layers with cross-stratification, lenses or small channels were observed. Fossils were found in all units, with the exception of the carbonate unit.

According to the stratigraphy, the stagnogleyic unit (2461–2680 cm.) is the oldest fluvial deposit in the study area (Figures 2 and 3). Inside this unit, at least three sedimentary beds with evidence of fluvial processes can be identified. The most recent bed probably includes several other beds because of their thickness. However, this bed could not be studied further due to its inaccessibility. The three sedimentary beds correspond to sands with planar cross-stratification and lenticular channels.

Three paleosols were recognized (14Bgk, 13G, 12Bg) in the stagnogleyic unit by means of their color pattern and pedogenic structure. Moreover, paleosol 14Bgk is separated from paleosol 13G by a sedimentary layer.

In general, paleosols of the stagnogleyic unit are poorly developed and their texture is mainly sandy (Figure 4), with a variable proportion of silt and mud and, a considerable content of gravels. Manganese (Mn) dendrites are found in the entire unit, even within fossils. Paleosols developed over sediments, filling old channels that are still visible at present (Figure 3b). Munsell color varies between 2.5 Y in the first 219 cm and 10 YR in the upper 30 cm.

Paleosol 14Bgk presents carbonate rhizoconcretions (Figure 3c) embedded in a brown matrix with columnar structure and numerous yellow-brown patches and black dendrite-manganese mottles (paleosol 14Bgk). A sand bed with disperse gravels (pebbles and cobbles) and channels with imbricated gravels overlies this paleosol.

Paleosol 13 G is incipient and some of its channels are preserved. Columnar structure is not well developed and is slightly friable. This paleosol contains remains of fossil mammoth (ribs, vertebrae and a defense).

Paleosol 12 Bg presents a high proportion of CaCO₃ associated with Mn channels, it is structured in blocks and, as in paleosol 13 G, is slightly

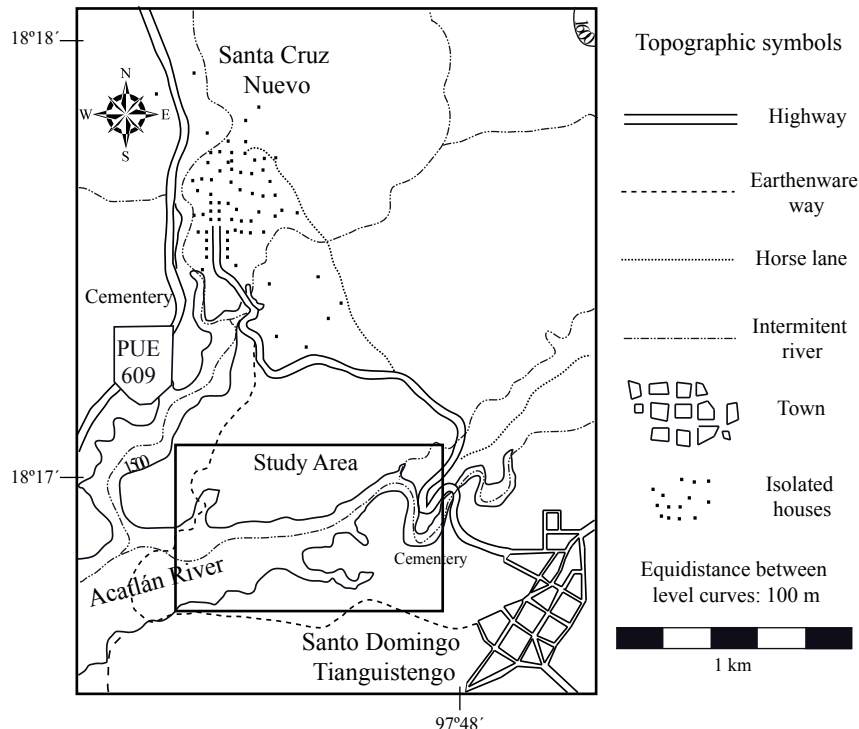


Figure 1. Location of the study area, to the south of the town Santa Cruz Nuevo, Puebla.

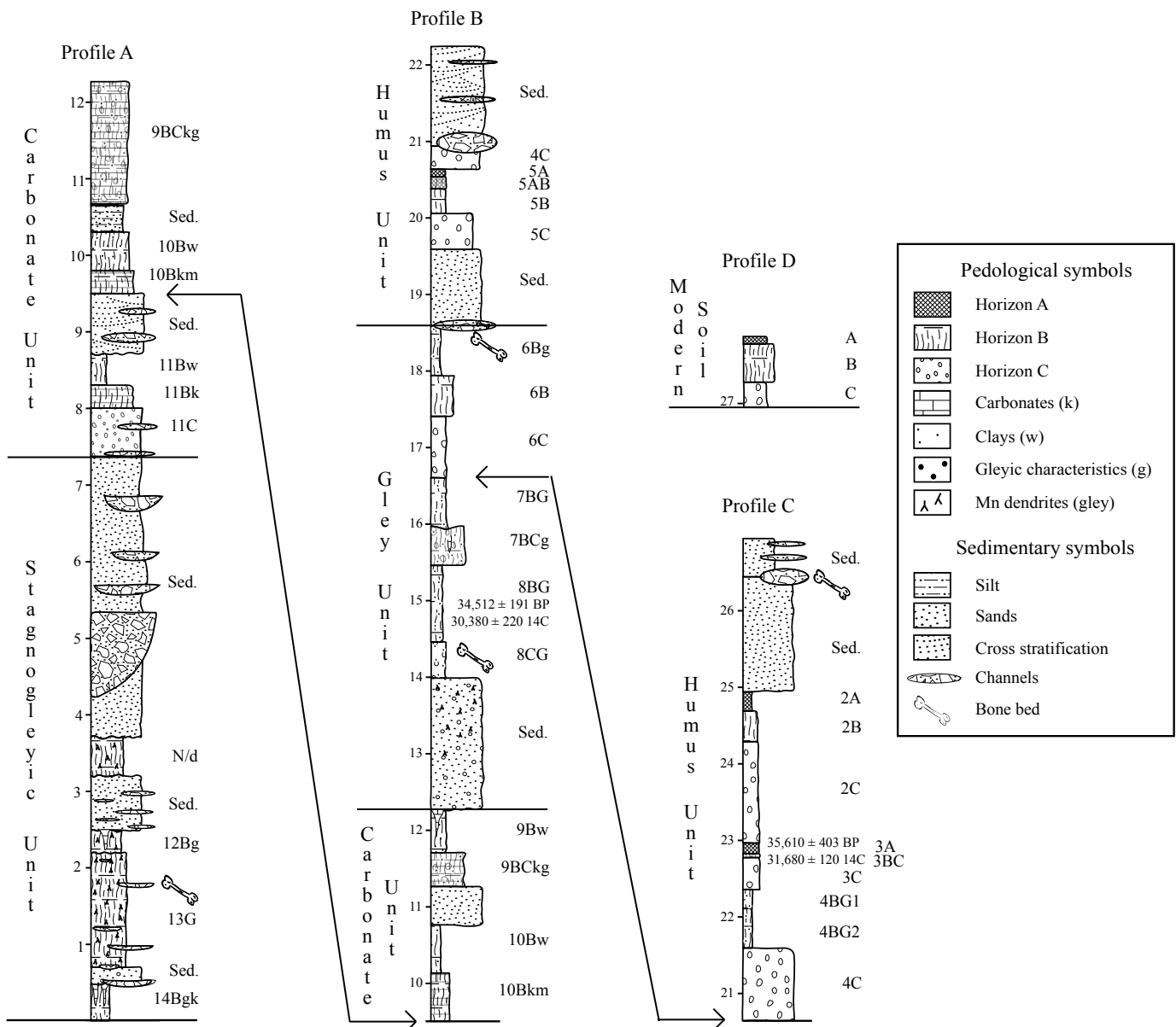


Figure 2. Pedostratigraphic units of Santa Cruz Nuevo. The correlative profiles are named with the letters A-D and the correlative horizons are joined through arrows. Ages are in radiocarbon years and before present (BP). Fossil beds or horizons are marked with a bone figure. Numbers on the left represent meters. Sed., sedimentary layer. N/d, undifferentiated horizon.

friable. Over the stagnogleyic unit lies a 367 cm sandstone bed with numerous channels. However, its position made it challenging to study.

At a micromorphological level, cavities, channels (some with chambers and fillings), manganese and iron (Fe) oxides are common in the stagnogleyic unit (Figure 5a). Little mesofauna evidence was found (Figure 5b).

The carbonate unit (1559–1973 cm) has brown-red colors (Munsell color corresponds to 10YR) with little alluvial evidence. Three poorly differentiated paleosols (11Bw-11Bk-11C, 10Bw-10Bkm, 9BCkg-9Bw) were recognized and separated by sedimentary beds. The 11Bw-11Bk-11C paleosol has a silt-clay texture, with prismatic blocks that can be broken into small blocks. Over this paleosol, the sedimentary bed corresponds to channeled sands.

Paleosol 10Bw displays a clay texture with small pebbles, several

yellow-brown patches, CaCO₃ in pores, and an angular block structure. Paleosol 10Bkm presents similar characteristics; however, it is more compact due to a higher proportion of CaCO₃ and a smaller number of patches. The subsequent layer is a silt layer identified as a weathered ash layer but with no visible structure.

Horizon 9BCkg presents a sand-silt texture with yellow-brown patches, pebbles and subangular blocks. Horizon 9Bw exhibits a silt-clay texture with a structural tendency to form blocks.

At a micromorphological level, high proportions of Mn and Fe oxides are evidenced in the carbonate unit. Although few channels and cavities can be observed, feeding evidence is common.

The gley unit (928–1559 cm) comprises three paleosols (8CG-8BG-, 7BCg-7BG, 6C-6B-6Bg) and a gleyic sediment. This unit is characterized by a toneless brown to greenish color (Figure 3d) and

brown-yellow patches. The Munsell color is 10YR except in paleosol 8CG-8BG, in which it is 2.5Y. The Mn dendrites are not as common as in the stagnogleyic unit.

Horizons 8CG-8BG displays a silt-clay texture, being finer in 8BG. The structure in 8CG is organized in blocks, whereas in 8BG it is granular. Horizon 7BCg presents a similar proportion of sands, silt and clay to that of 8CG-8BG. The structure consists of small angular blocks. Horizon 7Bg has a clay-silt texture and consists of small angular blocks than can be broken into granules. The texture of paleosol 6C-6B-6Bg is silt-muddy with an overlying clay layer; its structure is mainly organized in blocks.

This block structure is also evident at a micromorphological level (Figure 5c), in which fractures and Mn dendrites are evident, but not Fe oxides. No evidence of mesofaunal activity is observed, but a plant stem with secondary carbonate was preserved (Figure 5d).

The humus unit (143–828 cm) comprises four paleosols (5C-5B-5AB-5A, 4C-4Bg2-4Bg1, 3C-3BC-3A, 2C-2B-2A), three of which present a superficial Ah horizon. The Ah horizon is approximately 10-15 cm deep (Figure 3e). The structure consists of small blocks with a loamy texture (Figure 4) and scattered gravels. Sedimentary evidence of small channels and lamination can be observed. At the top of the humus unit, lenticular channels and parallel cross-stratification and

through cross stratification are present. The Munsell color is 10YR; however a strong pigmentation with dark humus is characteristic of the Ah horizons of this unit (Figure 3e).

The micromorphology evidences the presence of pedofeatures of Fe and Mn oxides, the latter being the least abundant. Unlike in the overlying gley unit, biogenic pores, some of them filled with mesofaunal feces and charcoal, were observed in this unit (Figures 5e and 5f).

The modern soil is poorly developed. The Ah horizon is 10 cm deep and presents a granular structure, a silt texture, and a great number of plant roots. The vegetation is primarily composed of cacti and magueys. Fractures and some pores can be appreciated at a micromorphological level. An absence of the ferruginous pedofeatures and Mn oxides present in all paleosols is noteworthy.

Two radiocarbon ages were obtained from the gley and humus units, $30,380 \pm 220$ ^{14}C years BP ($34,512 \pm 191$ cal. years BP) and $31,680 \pm 120$ ^{14}C years BP ($35,610 \pm 403$ cal. years BP), respectively. Both ages indicate that the deposit was formed at the end of marine isotope stage 3 (MIS 3).

The $\delta^{13}\text{C}$ values of humus and CaCO_3 (Table 1 and 2) are more negative at the base, and become less negative at the top of the pedostratigraphic section.

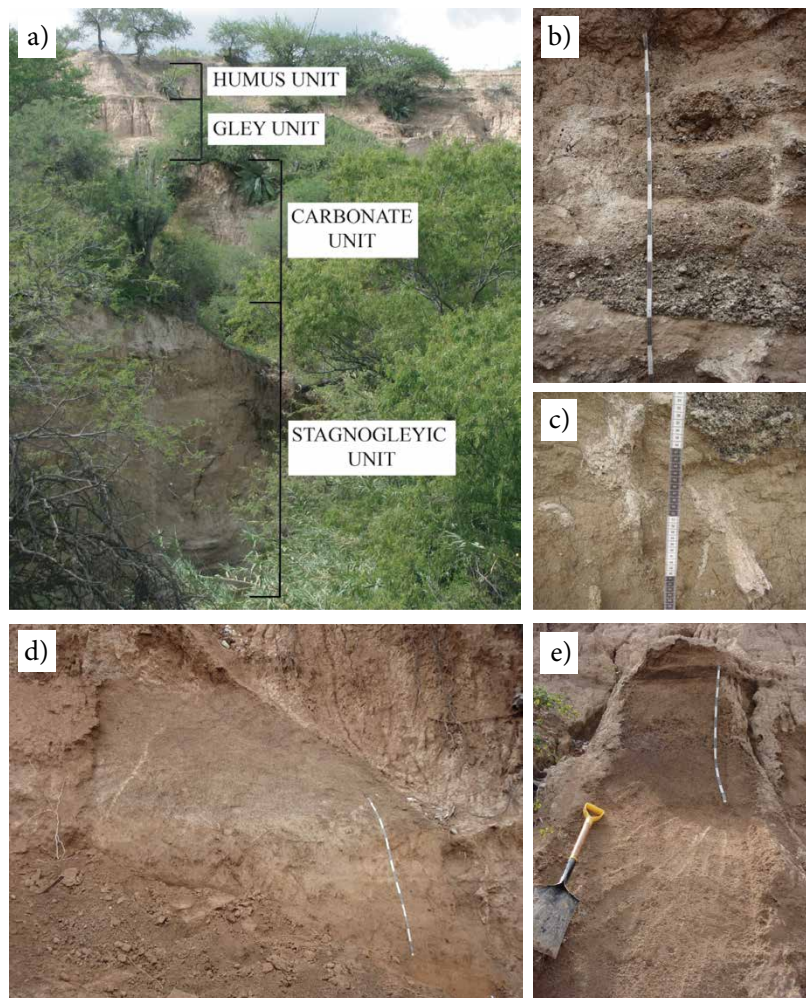


Figure 3. Macromorphological evidence in the pedostratigraphic units. a) A panoramic view of the arrangement and position of pedological units. b) Channel preservation in 13G horizon of the stagnogleyic unit. c) Rhizoconcretions in 14Bgk horizon from the stagnogleyic unit. d) A sedimentary bed of the gley unit. e) A profile (3A-3BC-3C) from the humus unit.

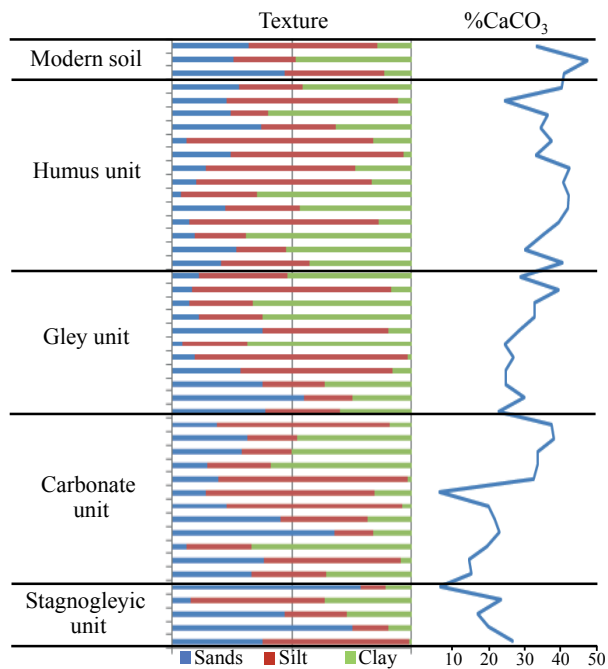


Figure 4. Textural analysis of the pedostratigraphic units.

Fossil findings

Three of the four recognized pedostratigraphic units in Santa Cruz Nuevo yielded fossil vertebrate remains. Mammoth remains (ribs, vertebrae, tusks and other unidentified anatomical parts) have been found in paleosol 3G of the stagnogleyic unit since 2002. Interestingly, fossils from this unit are dark, presumably due to an assimilation of manganese oxide.

The richest fossiliferous unit is the gley unit, where many microvertebrate fossils have been collected (Tovar and Montellano, 2006), particularly from horizon 8CG (Figure 2) and correlative beds. Fossils like salamanders (*Ambystoma* sp., Plethodontidae), toads (*Incilius* sp. and *Incilius occidentalis*), frogs (*Rana* sp.), turtles (*Gopherus* sp. cf. *G. berlandieri*), lizards (*Sceloporus* sp. cf. *S. grammicus*, *Sceloporus* sp. cf. *S. horridus*, Scincidae), snakes (*Conopsis* sp., *Lampropeltis* sp., *Leptodeira* sp., *Senticolis* sp., *Thamnophis* sp.), rabbits (*Sylvilagus floridanus*) and mice (*Neotoma mexicana*, *Peromyscus difficilis*) were commonly found in lenses throughout this unit.

A fossil horse tibia was collected from a channel in horizon 6Bg, at the top of the gley unit. However, an accurate dating could not be obtained due to low collagen content. At the same level but in lateral outcrops, several remains of fossil toads (*Incilius* sp. and *Incilius occidentalis*), spade foot toads (Scaphiopodidae), turtles (*Kinosternon* sp.), snakes (*Conopsis* sp., *Lampropeltis* sp., *Trimorphodon* sp., *Crotalus* sp.), giant armadillos (*Glyptotherium* sp.), rabbits (*Sylvilagus floridanus*), mice (*Neotoma mexicana*, *Reithromys* sp.), bears (Ursidae), cacomistles (*Bassariscus* sp. cf. *B. sumichrasti*), horses (*Equus conversidens*) and mammoths (*Mammuthus* sp.) have been recovered.

Toad (*Incilius* sp., *Incilius occidentalis*), turtle (*Kinosternon* sp.), snake (*Lampropeltis* sp., *Thamnophis* sp., *Crotalus* sp.), bird (*Cyrtonyx* sp., *Catharus* sp. cf. *C. occidentalis*, *Columba fasciata*, *Icterus* sp., *Pipilo* sp., *Salpinctes* sp. cf. *S. obsoletus*, *Dumetella* sp. cf. *D. carolinensis*, *Campylorhynchus* sp. cf. *C. rufinucha*, *Callipepla* sp. cf. *C. squamata*), giant armadillo (*Glyptotherium* sp.), rabbit (*Sylvilagus floridanus*), mice

(*Neotoma mexicana*) and deer (*Odocoileus* sp.) remains were collected from lenses in the sedimentary beds of the humus unit (Figure 2).

Considering all four units together, microvertebrates were more abundant than macrovertebrates: the number of megafaunal elements represents only 13% of the fossil bones recovered. The scarce megafaunal taxa recovered from the Santa Cruz Nuevo locality correspond to the Orders Cingulata, Artiodactyla, Perissodactyla, Proboscidea and the Ursidae family.

Most of the megafaunal bones are fragmented and therefore, non diagnostic. The most abundant elements are isolated osteoderms, antlers and teeth. The most complete remains include jaws and a fragmentary horse skull (Figure 6).

On the other hand, microvertebrate fossil bones are better preserved; a great number of limb bones are complete. However, the most abundant microvertebrate elements correspond to vertebrae. In addition, incomplete jaws with dental series and isolated teeth have also been found.

Finally, a turtle carapace scute with gnawing marks (Figure 7a) and root marks on frog bones (Figure 7b) are some of the most remarkable evidence of biological disturbance on the fossil remains of Santa Cruz Nuevo.

DISCUSSION

Paleosols and the environmental setting

The paleosols of Santa Cruz Nuevo provide evidence of incipient pedogenesis and sedimentary structures such as lenses or stratification. These sedimentary structures are common in alluvial soils, mainly in soils developed in floodplains (Gerrard, 1992).

The Mn dendrites, mainly found in the stagnogleyic unit but present in all units, are supporting evidence of temporary water saturation, probably originated from flooding (Gerrard, 1992; Schaetzl and Anderson, 2005). The poor development of paleosols, the presence of alluvial sedimentary structures (e.g., planar cross stratification and channels, combined with Mn dendritic mottles and gleyic color pattern) indicate that the paleosols of the stagnogleyic unit correspond to Gleyic Fluvisols (WRB, 2006).

Paleosols of the gley unit are Fluvisols and Gleysols. However, the exposition to floods appears to have been prolonged because no macroscopic evidence of Mn, a more mobile element than Fe (Gerrard, 1992; Schaetzl and Anderson, 2005), was found.

The incipient extent of differentiation in the carbonate unit suggests that these paleosols are Cambisols. On the other hand, the humus unit maintains their superficial A horizons suggesting a stability in the landscape. At the top of this unit, the presence of several small channels indicates the return to a fluvial activity. Above this unit there is a gap with no MIS 2 sediments preserved. The modern soil corresponds to Cambisol (WRB, 2006) originated in a xeric climate. It must be stressed that all paleosols show redoximorphic features, which are indicative of temporary water saturation. This kind of features is absent in the modern soil. Such absence points to a less drained environment or more frequent floods in the Pleistocene compared to the Holocene.

Fluvisols are not diagnostic of a particular climate (WRB, 2006) and composition of the vegetation was impossible to be determined because of an absence of phytoliths and pollen. However, past environments can also be reconstructed by means of stable carbon isotopes (e.g., Lounejeva-Baturina et al., 2006). In plants, carbon isotopic fractionation is associated with photosynthesis. Higher plants have three different metabolic pathways: C3, C4 and CAM. Values of $\delta^{13}\text{C}$ for C3 plants fall between -25 and -35‰, those for C4 range from -10 to -17‰, and CAM plants have a range of $\delta^{13}\text{C}$ values between those typical of C3

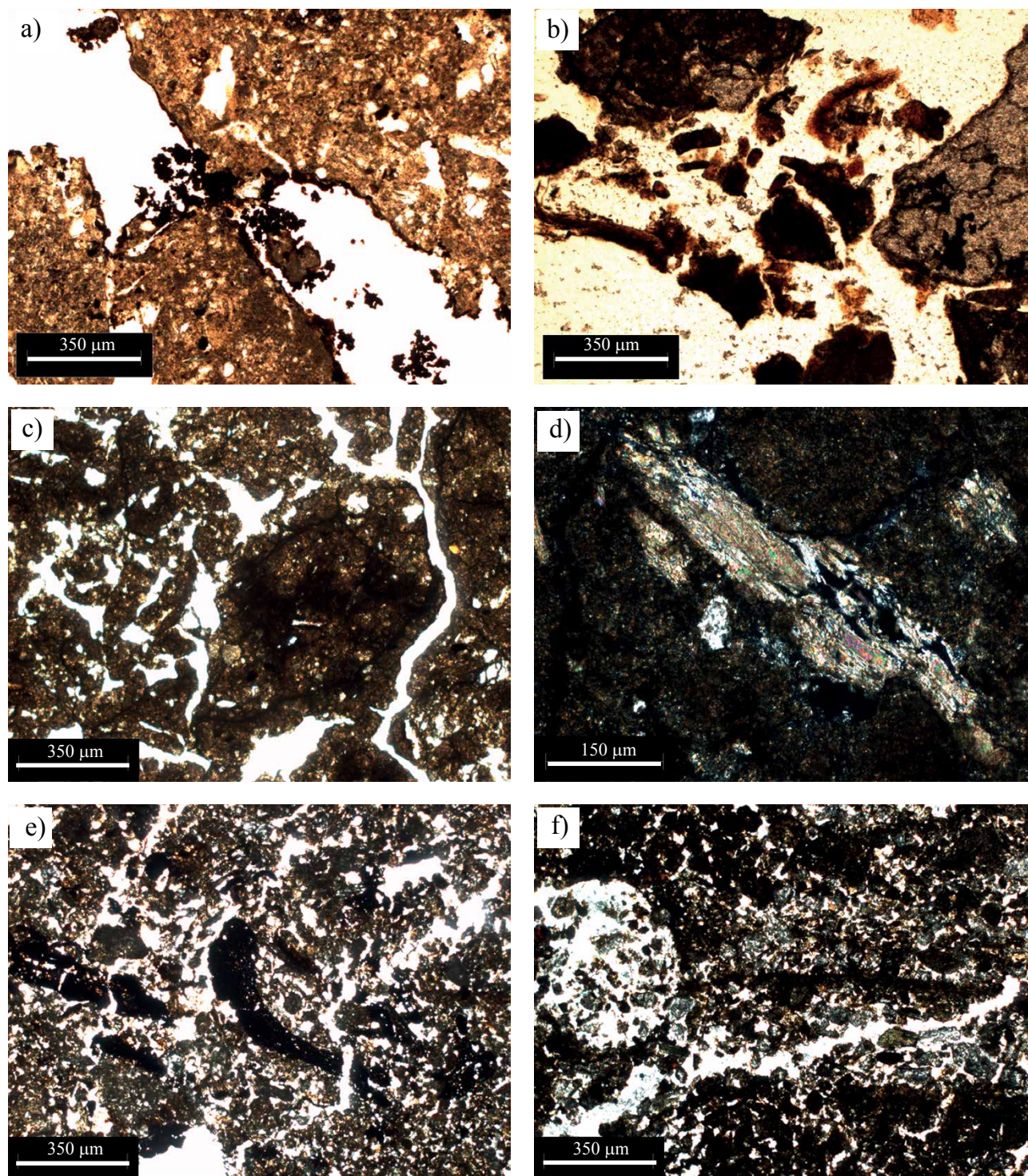


Figure 5. Micromorphology of the pedostratigraphic units. a) Mn cutan with the classic dendrite growing in the 12 Bg horizon of the stagnogleyic unit. b) Biotic remains in the horizon 10 Bw of the carbonate unit. Also, the blocky structure is evident. c) The blocky structure of the 8Bg horizon of the gley unit. d) A plant stem with secondary carbonate in the 8Bg horizon. e) Charcoal evidence in the 3A horizon of the humus unit. f) Biogenic evidence of mesofauna activity in the 3A horizon.

Table 1. The humus $\delta^{13}\text{C}$ values of selected horizons in the different units.

Unit	Horizon	$\delta^{13}\text{C}$
Stagnogleyic	14Bgk	-23.3
Gley	8BG	-22.52
	6BG	-22.30
Humus	3A	-19.5
	2A	-19.82
Modern soil	Ah	-18.46

and C4 plants because they are facultative. CAM plants have values similar to those of C4 plants during active acidification, *i.e.*, when plants are not well watered (Edwards and Walker, 1983). C3 plants are typical of humid climates, whereas C4 plants characterize warm and dry areas.

The analysis of $\delta^{13}\text{C}$ in paleosol humus and secondary carbonates shows a trend to less negative values at the top of the pedosequence (Tables 1 and 2), with values ranging between -22‰ and -23‰ in the lower three units (stagnogleyic, gley and carbonate) to -19.82‰ and -19.5‰ in the humus unit. The $\delta^{13}\text{C}$ of modern soil is -18.46. Thus, we observe a tendency towards less negative $\delta^{13}\text{C}$ values in the modern soil compared to Pleistocene paleosols. In Santa Cruz Nuevo, this tendency towards drier environments is less conspicuous than in other Pleistocene-Holocene sequences of central and southern Mexico (*e.g.*, Canul-Montañez, 2008, Lounejeva-Baturina *et al.*, 2006, Lozano-García *et al.*, 2005, Tovar *et al.*, 2013, 2014).

The $\delta^{13}\text{C}$ values correspond to a mixed vegetation with a preponderance of C3 plants at the base (stagnogleyic unit) and an increase in C4 plants at the top (humus unit). At present, modern soil in Santa Cruz Nuevo supports a shrubland vegetation with numerous CAM plants such as cacti and magueys with no evidence of grasses, except for the cultivated areas.

Fossil vertebrates of Santa Cruz Nuevo

The fossil vertebrates of Santa Cruz Nuevo were highly useful in the reconstruction of past environments in the study area because they

Table 2. Secondary CaCO_3 values in paleosols.

Horizon	Pedological unit	$\delta^{13}\text{C}_{\text{VPDB}}$ (‰)	$\delta^{18}\text{O}_{\text{VPDB}}$ (‰)	Enrichment factor -15
13 G	Stagnogleyic	-6.94	-8.51	-21.94
9Bkm	Carbonate	-8.22	-11.3	-23.22

presented clues to the conditions in which the organisms lived, their position in the food chain and their interaction with other species. In addition, the analysis of skeletal elements traces the history of the individual from its death, transport, burial, and finally, the discovery of the site where the remains lay (Behrensmeyer, 1984).

The paleoenvironment reconstruction in the study area was developed according to the ecological requirements of modern analogs and the published data on habitat reconstructions of extinct fauna. Fossil vertebrates were found in three paleopedological units (stagnogleyic, gley and humus units) and were more abundant in the last two.

Bone elements of *Mammuthus* sp. most likely belonging to a single specimen (since 2002, different parts of the skeleton have been discovered) were uncovered in the stagnogleyic unit. These remains have not yet been removed from the site due to extraction difficulties. The animal probably died close to the study area, because most of the skeletal elements remain together, although not articulated. Agenbroad (1984) suggested that the preferred habitat of mammoths was open areas as grasslands. The present work suggests that the grassland composition had a considerable proportion of C3 grasses as evidenced by a $\delta^{13}\text{C}$ signature.

In the gley and humus units, fossils are associated to fluvial sediments or incipient paleosols. The most abundant orders correspond to animals of amphibian habits or those living close to rivers.

Behrensmeyer (1982) stated that fossils found inside channels can be interpreted as allochthonous (outside the animal distribution area), whereas fossils found in a finely grained matrix characteristic of floodplains are inferred as autochthonous (within the area where the animal lived). Because microvertebrates have been found in fine sediments and fragile bones break easily during water transportation (Korth, 1979), it is assumed that the microvertebrate association in



Figure 6. Skull of *Equus conversidens* collected in the gley unit of Santa Cruz Nuevo. The scale bar represents 10 cm.

Santa Cruz Nuevo is para-autochthonous, *i.e.*, within the animal distribution area. As previously mentioned, megafaunal remains are less abundant than those of microvertebrates, with only four mammal orders present (Xenarthra, Uranotheria, Perissodactyla and Carnivora). Most of the macrovertebrate fossils correspond to skull fragments, jaws and isolated teeth, which, according to Voorhies (1969), are not transported for long distances.

A large sample of microvertebrates was collected from the gley unit (Figure 8). Some of the identified taxa, *Ambystoma* sp. and *Kinosternon* sp. are strictly associated with fresh water (Zug *et al.*, 2001); other taxa such as Scaphiropodidae, *Gopherus* sp. cf. *G. berlandieri*, *Sceloporus* sp. cf. *S. horridus*, *Senticolis* sp., *Peromyscus difficilis*, *Equus conversidens* and *Mammuthus* sp. are restricted to dry areas in ecosystems such as shrublands, dry spiny forests, grasslands or deserts (Smith, 1939; Hibbard and Taylor, 1960; Ceballos-González and Galindo-Leal, 1984; Benítez-Gálvez, 1997; Agenbroad, 1984); and others like *Incilius occidentalis*, *Sceloporus* sp. cf. *S. grammicus*, *Conopsis* sp., *Leptodeira* sp., *Neotoma mexicana*, *Bassariscus* sp. cf. *B. sumichrasti* inhabit dry or temperate areas. Dry ecosystems include shrublands, spiny forests and grasslands; temperate ecosystems are coniferous and/or oak forests (Duellman, 1966; Ceballos-González and Galindo-Leal, 1984; Benítez-Gálvez, 1997). Some eurytopic taxa are present in the sample: *Lampropeltis* sp., *Thamnophis* sp., *Crotalus* sp., *Sylvilagus floridanus*, *Reithromys* sp. (Lee, 1996; Benítez-Gálvez, 1997). Due to their high tolerance to wide ecological variations, eurytopic taxa are not useful in environment determination.

According to McNab (1985), *Glyptotherium*, the giant armadillo, inhabited tropical to warm-temperate areas, eating leaves along water bodies (Gillete and Ray, 1981). However, the $\delta^{13}\text{C}$ analysis of glyptodont teeth from El Cedral, San Luis Potosí, Mexico, exhibited a mixed diet (C3/C4) of the members of this taxon. The large C4 plant consumption of the El Cedral *Glyptotherium* suggests that this genus was, preferentially, a grassland grazer (Pérez-Crespo *et al.*, 2012). The study of the fossil giant armadillos of Santa Cruz Nuevo supports the interpretation of Pérez-Crespo *et al.*, (2012).

The humus unit shares many species with the gley unit (Figure 8). The species or genera inhabiting dry spiny forests, shrublands and/or grasslands are *Salpinctes* sp. cf. *S. obsoletus*, *Dumetella* sp. cf. *D. carolinensis*, *Campylorhynchus* sp. cf. *C. rufinucha*, *Callipepla* sp. cf. *C. squamata*, and *Glyptotherium* sp. (Peterson and Chalif, 2008; Pérez-Crespo *et al.*, 2012). The temperate species are *Catharus* sp. cf. *C. occidentalis* and *Columba fasciata* (Peterson and Chalif, 2008). The species distributed in dry and temperate areas are *Incilius occidentalis*,

Cyrtonyx sp., *Neotoma mexicana* and *Odocoileus* sp. (Duellman, 1966; Ceballos-González and Galindo-Leal, 1984; Peterson and Chalif, 2008). The eurytopic species are *Lampropeltis* sp., *Thamnophis* sp., *Crotalus* sp., *Icterus* sp., *Pipilo* sp., *Sylvilagus floridanus* (Benítez-Gálvez, 1997; Peterson and Chalif, 2008). In the humus unit only one aquatic genus (*Kinosternon* sp.) is found.

The assemblages of both gley and humus units present similar fauna. Although some temperate forest elements are present in both groupings, most of the identified taxa inhabited dry areas such as xeric shrublands or grasslands, suggesting that these kinds of vegetation were predominant during the end of the Pleistocene, although the idea of a mosaic habitat is not dismissed. With the use of both fossil and recent microvertebrates it was noticed that there are no extinct microvertebrates in the area and that the eradicated fauna belong to herpetofauna (Tovar and Montellano, 2006). Salamanders (Families Ambystomatidae and Phletodontidae), skinks (Family Scincidae) and two kinds of turtles (Families Bataguridae and Testudinidae) are absent in the study area at present.

Although several fossil taxa have been eradicated from the Santa Cruz Nuevo area, it is worth mentioning that most of the microvertebrate fossils in particular, still have extant representatives in the study area, and that this pattern has also been observed in other localities (Parmley and Pfau, 1997).

The results herein presented suggest that the stagnogleyic unit ($\delta^{13}\text{C}$ -23.3‰ to -21.94‰) corresponds to a grassland with an abundance of C3 grasses and a minor proportion of C4 grasses and other C4 plants. Both kinds of grasses might have represented a food source for the mammoth, which has been reported as a mixed-feeder (Pérez-Crespo *et al.*, 2009; Nunez *et al.*, 2010).

The gley unit (30,380±220 ^{14}C years BP) presents $\delta^{13}\text{C}$ values (-22.52‰ to -22.3‰) similar to those of the stagnogleyic unit. The occurrence of certain taxa suggests the possible presence of either grassland or shrubland in the area. The evidence assembled here leads to interpret the paleoenvironment as a grassland area, with a great proportion of C3 grasses and patches of shrubland, in which the dominant vegetation was composed by CAM plants such as cacti, magueys and other succulent plants. CAM plants are particularly adapted to semi-arid environments and when the water supply is abundant, they directly fix atmospheric CO_2 during the day through ribulose 1,5-biphosphate (RBP) carboxilase as C3 plants do (Edwards and Walker, 1983).

Water may not have been an abundant resource in the area; however, it is well documented that flooded water can generate a temporary wetland environment in lowlands, regardless the climate.

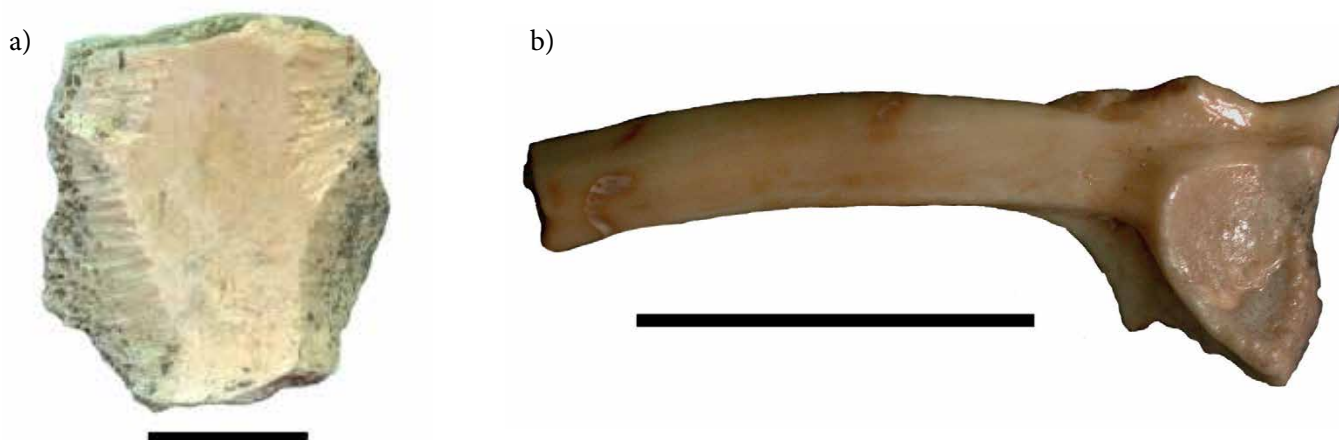


Figure 7. Biotic modification in fossil bones. a) Scute of *Gopherus* sp. with gnawing marks. b) Root marks over a frog ilion. The scale bar represents 1 cm.

Identified taxa	Ecosystems						Pedological unit
	DDF	SF	XS	G	OF	CF	
<i>Incilius occidentalis</i>	x		x		x	x	Gley and Humus
<i>Gopherus</i> cf. <i>G. berlandieri</i>			x				Gley
<i>Sceloporus</i> cf. <i>S. grammicus</i>	x	x	x				Gley
<i>Sceloporus</i> cf. <i>S. horridus</i>			x				Gley
<i>Conopsis</i> sp.			x	x	x	x	Gley
<i>Leptodeira</i> sp.			x		x		Gley
<i>Senticolis</i> sp.			x				Gley
<i>Trimorphodon</i> sp.			x	x	x	x	Gley
<i>Crotalus</i> sp.	x	x	x		x	x	Gley and Humus
<i>Cyrtonyx</i> sp.			x	x	x	x	Humus
<i>Catharus</i> cf. <i>C. occidentalis</i>					x	x	Humus
<i>Columba fasciata</i>					x	x	Humus
<i>Salpinctes</i> cf. <i>S. obsoletus</i>		x	x				Humus
<i>Dumetella</i> cf. <i>D. carolinensis</i>		x	x				Humus
<i>Campylorhynchus</i> cf. <i>C. rufinucha</i>		x	x	x			Humus
<i>Callipepla</i> cf. <i>C. squamata</i>			x				Humus
<i>Glyptotherium</i> sp.			x				Gley and Humus
<i>Sylvilagus floridanus</i>			x	x	x	x	Gley and Humus
<i>Neotoma mexicana</i>		x	x	x	x	x	Gley and Humus
<i>Peromyscus difficilis</i>		x	x				Gley
<i>Reithromomys</i> sp.				x			Gley
<i>Ursidae</i>					x	x	Gley
<i>Bassariscus</i> cf. <i>B. sumichrasti</i>			x		x	x	Gley
<i>Odocoileus</i> sp.			x			x	Humus
<i>Equus conversidens</i>			x	x			Gley
<i>Mammuthus</i> sp.			x	x			Gley

Figure 8. Kinds of vegetation associated to the identified fossil taxa from the gley and humus units. The eurytopic species are not included. DDF: Dry deciduous forest, SF: Spiny forest, XS: Xeric shrubland, G: Grassland, OF: Oak forest, CF: Coniferous forest.

Gleysols, soils characteristic of the gley unit, are formed in nearly all climates ranging from perhumid to arid and are associated with topographic lows (WRB, 2006) where water is available and exhibits a negative signal.

The humus unit (31,680±120 ¹⁴C years BP) shows higher $\delta^{13}\text{C}$ values (-19.82‰ to -19.5‰), supporting an increase of C4 plants and probably warmer conditions alongside a decrease in water supply.

Chronology of Santa Cruz Nuevo and correlation with other records at the end of MIS 3 in south-central Mexico

The pedosequence of Santa Cruz Nuevo comprises the end of MIS 3, around 30,000 ¹⁴C years BP. The analysis of the environmental conditions, as previously mentioned, suggested a transition from dry to drier conditions.

Santa Cruz Nuevo is located close to the locality of Axamilpa, Tepexi de Rodríguez, Puebla, Mexico. Axamilpa is younger than Santa Cruz Nuevo and the prevailing environmental conditions, at the end of MIS 3, was a temperate weather (a forest) changing to a semi-arid climate (Tovar et al., 2014) as observed at present, demonstrating a dry phase in the region.

However, most publications, either on lakes or paleosol profiles, have previously suggested in their climatic interpretations the presence of dry periods around >30,000 years BP (Figure 9, Table 3). According to $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values in snail shells, before 36,000 ¹⁴C BP the paleoclimate in the Upper Barranca Caulapan in Valsequillo was slightly drier than at present. After that date, weather conditions became drier up to the 28,000 to 20,000 ¹⁴C years BP interval, when conditions

became cooler and wetter (Stevens et al., 2012). Lozano-García and Xelhuantzi-López (1997) suggested a subhumid cooler climate with drier periods during the interval of ca. 35,000 to ca. 20,000 ¹⁴C years BP in the Texcoco Lake.

The analyses of paleosols, $\delta^{13}\text{C}$, and fossil pollen from the subunit TX2 (30,189 to 51,798 cal. years BP) in Huexoyucan and the sections Tlalpan and Mammut (38,000 to 29,000 ¹⁴C years BP), in Tlaxcala, Mexico, suggest the presence of a forest vegetation with a mean annual temperature of 7-8 °C, with cold and humid conditions (Sedov et al. 2009; Solís-Castillo et al., 2012). In the Teotihuacan Valley, Estado de Mexico, the pedostratigraphic level SP4 is correlated with TX2. There, the pedogenesis was humid, indicating a temperate forest environment. However, there is also evidence of dry seasons such as vertic processes, carbonate precipitation and bioturbation (Solleiro-Rebolledo et al., 2011).

At approximately ~52,000 cal. years BP, a forest of *Quercus*, *Alnus*, Cupressaceae and *Fraxinus* was established in the Zacapu basin, Michoacán, Mexico; however, around 42,000 cal. years BP and until a hiatus around 30,000 years cal. BP, drier conditions took place according to the reported presence of high percentages of Poaceae, Asteraceae, Amaranthaceae and Cyperaceae (Correa-Metrio et al., 2012).

For the Chalco lake, Estado de Mexico, during 34,000 and 31,500 ¹⁴C years BP, the diatom assemblage suggests that the lake was shallow and alkaline. After 31,500 ¹⁴C years BP, the lake experienced a reduction in its water level becoming alkaline and saline (Caballero-Miranda, 1997). While for the Cuitzeo lake, Michoacán, the absence of diatoms in the sedimentary record at around 35,000 years BP sug-

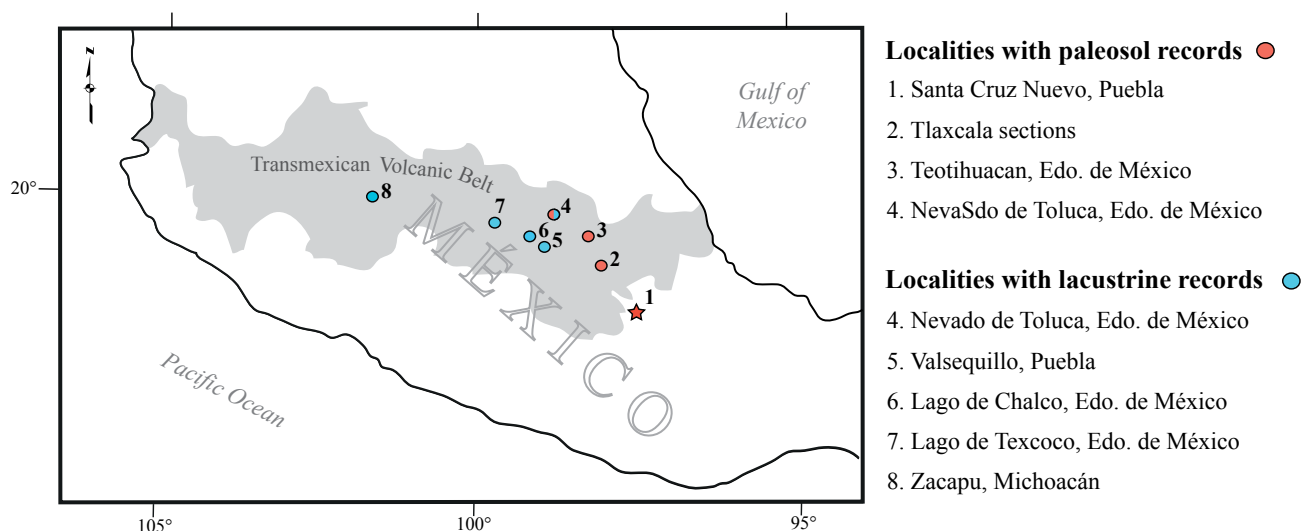


Figure 9. Localities in the Transmexican Volcanic Belt with paleoenvironmental records of marine isotope stage 3 and the study site, Santa Cruz Nuevo, marked with a star. Records correspond to paleosol and lacustrine studies.

gests a very low water level in the lake (Israde-Alcántara *et al.*, 2002).

In the Zacango sequence, northern flank of Nevado de Toluca, Mexico, the pollen record suggests that after the 37,000 years BP eruption of the Nevado de Toluca volcano, there was a shallow and stagnic pond surrounded by grassland (Caballero *et al.*, 2001). However, the pedological features of pedocomplex PT3 in Nevado de Toluca, dated at $35,650 \pm 1200$ ¹⁴C years BP, indicate processes typical of Andosols which are formed under forest vegetation (Sedov *et al.*, 2001).

Most MIS 3 records come from lakes and paleosols. Pleistocene vertebrate fossils were very abundant in Mexico however the lack of instrumental dating and stratigraphic control for many localities make the chronological comparison between localities of the same age practically impossible, particularly when we try to compare them in a millennial scale.

On the other hand, lake records are especially useful because their continuous entry allows researchers to recognize regional climatic changes in a known scale, while paleosols are mere glimpses of specific moments in time. However, the study of paleosols also gives clues on local processes and help in the understanding of the dynamics of local communities.

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Table 3. Published paleoenvironmental records for the end of marine isotope stage 3 in south-central Mexico. SCN: Santa Cruz Nuevo.

#	Site	Record carriers	Paleoenvironmental interpretation	References
1	SCN	Micromorphology, carbon isotopes, fossils	Dry conditions	This study
Paleosol proxies				
2	Tlalpan and Mammut sections (TX2), Tlaxcala	Mineralogical analyses and micromorphology	Cold and humid conditions	Sedov <i>et al.</i> 2009, Solís-Castillo <i>et al.</i> , 2012
3	Río San Pablo, Teotihuacán, Estado de México	Micromorphology, physical and chemical analyses	Humid with dry seasons	Solleiro-Rebolledo <i>et al.</i> , 2011
4	Nevado de Toluca, Estado de México	Micromorphology, physical and chemical analyses	Humid forest environments	Sedov <i>et al.</i> , 2001
Lacustrine proxies				
4	Nevado de Toluca, Estado de México	Pollen	Dry conditions	Caballero <i>et al.</i> , 2001
5	Barranca Caulapan, Valsequillo, Puebla	Carbon and oxygen isotopes in molluscan shells	Little drier than today	Stevens <i>et al.</i> , 2012
6	Lake Chalco, Estado de México	Diatoms	Alkaline, shallow lake with turbid waters	Caballero-Miranda, 1997
7	Lake of Texcoco, Estado de México	Pollen	Subhumid-cooler climate with drier periods	Lozano-García and Xelhuantzi-López, 1997
8	Zacapu, Michoacán	Pollen	Dry conditions	Correa-Metrio <i>et al.</i> , 2012

preparation of thin sections, René Alcalá for his support in the grain size determination of paleosols and Kumiko Shimada for her help in TOC determination. Pedro Morales and Edith Cienfuegos (Laboratorio de Espectrometría de Isótopos Estables [LUGIS], Universidad Nacional Autónoma de México) contributed with the stable carbon isotope composition of paleosol humus.

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Dark humic alluvial paleosols in Central and Southern Mexico: Micromorphological indicators of Late Pleistocene megafauna habitats

Paleosuelos aluviales con humus oscuro en el Centro y Sur de México: indicadores micromorfológicos de los hábitats de la megafauna del Pleistoceno tardío

Paleosolos aluviais com húmus escuro no Centro e Sul do México: indicadores micromorfológicos dos hábitats da megafauna do Pleistocénico tardio

AUTHORS

Tovar R.E.^①
rosae.tovar@ciencias.unam.mx

Sedov S.^②

Solís B.^②

Solleiro E.^②

⑥ Corresponding Author

^① Posgrado en Ciencias de la Tierra, Instituto de Geología, UNAM, Ciudad Universitaria s/n, Delegación Coyoacán, México, 04510.

^② Instituto de Geología, UNAM, Ciudad Universitaria s/n, Delegación Coyoacán, México, 04510.

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ABSTRACT

During the Late Pleistocene, Mexico had a richer fauna than today with many different forms of megafauna that are now extinct. However, the ecosystems they inhabited and the particular ecological niches that they occupied are still poorly understood. Most of the findings of Pleistocene megafauna have been in alluvial deposits that present rich opportunities for paleoecological studies using paleopedological records. Floodplain paleosols commonly are poorly developed. However, micromorphological analysis provides information about the grade of development of the soil at a microscale, discriminating between genetic and sedimentary processes; thus helping in the identification of the environmental setting in which they formed. We analyzed the micromorphology of six pedogenetic units in the sequences of Santa Cruz Nuevo and Axamilpa, in the south of Puebla, and Huexoyucan, in the state of Tlaxcala. These pedosequences correspond to the second half of marine isotopic stage 3 (MIS3), MIS2 and the early Holocene. All studied units are characterized by strong pigmentation with dark humus. The micromorphological analysis of MIS3 paleosols reveals aquatic conditions with evidence of freshwater biota and microlamination as well as pedogenetic features of hydrogenic carbonate precipitation and redoximorphic processes. The dark paleosols of MIS2 and the early Holocene demonstrate signs of stronger coprogenic aggregation, weathering and fewer gleyic features. Comparison with modern soils shows that the latter were formed under better-drained, aerated conditions that exclude redoximorphic processes. We conclude that the dark colored Pleistocene paleosol units are indicative of different paleo-landscapes: wetlands in the MIS3 and moist meadows in MIS2 – early Holocene. The swampy ecosystems could play an important role as a megafauna habitat.

RESUMEN

En el Pleistoceno Tardío, México tenía una diversidad faunística más rica que en la actualidad, con diferentes formas de megafauna, hoy extinta. Sin embargo, los ecosistemas que habitaron y determinados nichos ecológicos que ocupaban son poco conocidos. Los hallazgos más numerosos de la megafauna del Pleistoceno han sido en depósitos aluviales, los cuales son registros paleoecológicos importantes que representan una excelente oportunidad para ser estudiados. Los paleosuelos aluviales regularmente son poco desarrollados, sin embargo, el análisis micromorfológico proporciona información relevante sobre el grado de desarrollo del suelo a una microescala, permitiendo discriminar entre los procesos edafogenéticos y sedimentarios; ayudando con ello a la identificación de la configuración del medio ambiente en el que se formaron. Nosotros analizamos la micromorfología de seis unidades edafogenéticas en las secuencias de Santa Cruz Nuevo y Axamilpa, en el sur de Puebla y Huexoyucan, en el estado de Tlaxcala. Estas edafosecuencias corresponden a la segunda mitad de la etapa isotópica marina 3 (MIS3), etapa isotópica marina 2 MIS2 y al Holoceno Temprano. Todas las unidades estudiadas se caracterizan por una fuerte pigmentación con humus oscuro. El análisis micromorfológico de los paleosuelos de MIS3 revela condiciones acuáticas con evidencias

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de biota de agua dulce, como también microlaminaciones de precipitación de carbonatos hidrogénicos y procesos redoximórficos. Los paleosuelos oscuros de MIS2 y el Holoceno Temprano muestran fuerte agregación coprogénica, intemperismo y pocos rasgos gleycos, presentando fuertes diferencias con los suelos modernos. Los suelos modernos se formaron en condiciones aireadas, con un mejor drenaje que excluyen los procesos redoximórficos. Llegamos a la conclusión de que las unidades de paleosuelos del Pleistoceno de color oscuro son indicativos de diferentes paleopaisajes: humedales pantanosos en la MIS3 y praderas húmedas desde MIS2 hasta el Holoceno Temprano. Los ecosistemas pantanosos podrían representar un importante hábitat para la megafauna del Pleistoceno.

RESUMO

No Pleistocénico tardío, o México apresentava uma diversidade faunística mais rica que na actualidade, com diferentes formas de megafauna, hoje extinta. Sem dúvida, os ecossistemas que habitaram e determinados nichos ecológicos que ocupavam são pouco conhecidos. A maioria dos numerosos achados da megafauna do Pleistocénico foi em depósitos aluviais, que representam registos importantes paleoecológicos pelo que constituem uma excelente oportunidade para serem estudados. Os paleosolos aluviais são geralmente pouco desenvolvidos, pelo que a análise micromorfológica proporciona, sem dúvida, informação relevante sobre o grau de desenvolvimento do solo à microescala, permitindo distinguir entre os processos pedogenéticos e sedimentares, ajudando com isso à identificação da configuração do ambiente em que se formaram. No nosso estudo, procedeu-se à análise da micromorfologia de seis unidades pedogenéticas nas sequências de Santa Cruz Nuevo e Axamilpa, no Sul de Puebla e Huexoyucan, no estado de Tlaxcala. Estas pedosequências correspondem à segunda metade da etapa isotópica marinha 3 (MIS3), etapa isotópica marinha 2 MIS2 e ao Holocénico Inicial. Todas as unidades estudadas caracterizavam-se por uma forte pigmentação com húmus escuro. A análise micromorfológica dos paleosolos de MIS3 revelou condições aquáticas com evidências de biota de água doce, bem como microlaminações de precipitação de carbonatos hidrogenados e processos redoximórficos. Los paleosolos oscuros de MIS2 e o Holocénico Inicial apresentavam forte agregação cuprogénica, intemperismo e poucas características gleycos, apresentando grandes diferenças para os solos modernos. Os solos modernos formaram-se em condições de arejamento, com uma melhor drenagem que excluem os processos redoximórficos. Deste estudo concluímos que as unidades de paleosolos do Pleistocénico de cor escura são indicativas de diferentes paleopaisagens: zonas húmidas pantanosas na MIS3 e prados húmidos desde MIS2 até ao Holocénico Inicial. Os ecossistemas pantanosos poderão representar um importante habitat para a megafauna do Pleistocénico.

KEY WORDS
Palaeoenvironments,
 $\delta^{13}\text{C}$, Puebla,
Tlaxcala, MIS3,
MIS2

**PALABRAS
CLAVE**
Paleoambientes,
 $\delta^{13}\text{C}$, Puebla,
Tlaxcala, MIS3,
MIS2

**PALAVRAS-
CHAVE**
Paleoambientes,
 $\delta^{13}\text{C}$, Puebla,
Tlaxcala, MIS3,
MIS2

1. Introduction

Paleosols provide important proxy information about past environments, and are therefore widely used for reconstructing Pleistocene landscapes. A special value of paleopedological records is their high spatial resolution (Targulian and Goryachkin 2004) which provides possibilities for the reconstruction of the geographical variability and distribution of paleoecosystems. Such reconstructions are important for understanding biodiversity. Nowadays, Mexico is placed fifth among the world's most megadiverse countries (Llorente-Bousquets and Ocegueda 2008), with a greater richness concentrated in the south of the country due to the convergence of many mountain ranges (Espinosa et al. 2008). The biota was also rich during the Pleistocene. Martin (2005) pointed to the fact that megaherbivorous assemblages were more diverse during the Pleistocene than the current Africa assemblages. Ceballos et al. (2010), analyzing the current and fossil Mexican mammal record, concluded that communities of Pleistocene mammals were richer than today.

Also, the analysis of the North American continental fossil record points to the hypothesis that the environment was heterogeneous during the Pleistocene with no analogs in the Holocene. Manifestations of this heterogeneity are the plant and animal communities from different ecosystems that come together from their southern and northern ranges (FAUNMAP Working Group 1996). These associations are named disharmonic or ecological incompatible assemblages (Fay 1988; Graham and Lundelius 1989; Lundelius 1985). We believe paleosols are capable of highlighting the paleoenvironmental biodiversity and give hints about the habitats of extinct elements of Pleistocene biota, including megafauna.

Earlier Pleistocene paleosols in Mexico have been studied in the volcanic highlands where regular deposition of tephra provides development of paleosol series with variable timescales (Solleiro-Rebolledo and Sedov 2011). This research aims to identify and investigate paleosols in southern Mexico, where the Quaternary environmental history is still poorly documented despite recent rich paleontological findings.

In this non-volcanic terrain we focused on the alluvial geosystems for the following reasons:

- They are dynamic, with alternating phases of stability, erosion and sedimentation, and provide local conditions for soil development and their posterior burial.
- They are closely associated (often in one exposure) with paleontological findings and other biotic proxies like stable carbon isotopes, phytoliths, and aquatic microfossils.

In Mexico, several studies of the alluvial paleosol-sedimentary sequences have been undertaken in the last decades, most of them focusing on Holocene profiles that contained records of both natural environmental change and human-induced landscape dynamics (e.g. Sedov et al. 2010). A few studies also dealt with the Pleistocene sequences trying to establish

their links to the regional climate fluctuations (Solís-Castillo et al. 2012; Tovar et al. 2014).

Within these studies, humus-rich, dark-colored Late Pleistocene paleosols were found in alluvial geosystems at different elevations. We hypothesize that these paleosols provide a record about ancient riverine ecosystems that were widespread during the Last Glacial period and considerably diminished later. These paleosols seem to be part of the broader paleopedological tendency of humus-rich paleosol development that occurred over a wide range of regions of North America during Late Pleistocene and the Pleistocene-Holocene transition (for example, the strata known as Black Mats in the southwest of the USA, corresponding to the Younger Dryas (e.g. Haynes 2008)). Thus they deserve a special pedogenetic and paleoecological study.

The alluvial paleosols are often immature and syn-sedimentary, so extracting pedogenetic information from standard physical and chemical analyses is difficult. Micromorphology is of primary importance for studying the pedogenesis in these paleosols, as it is an adequate tool for the

- Identification of incipient, poorly developed features of soil forming processes and
- Discrimination between pedogenetic and sedimentary phenomena, including identification of redeposited soil materials (pedosediments).

The objective of this paper is to compare the micromorphology of three alluvial sequences of late Pleistocene age at different altitudes in Central and Southern Mexico in order to reconstruct past environments.

2. Material and Methods

In order to compare the paleopedological records in the different altitudinal zones of tropical Mexico, we studied alluvial soil-sedimentary sequences in two regions of the central and southern parts of the country with an elevation difference of about 2600 m. Three sections were studied in total: Huexoyucan (Tlaxcala State), Santa Cruz Nuevo and Axamilpa (Puebla State) (Figure 1). Huexoyucan is located in the Transmexican Volcanic Belt, in the Tlaxcala Block, which is part of Puebla-Tlaxcala Basin, between the coordinates 19°27'41.3"N, 98°18'52.5" W, and 19°22'16.7"N, 98°16'47.4"W, at around 2500

mamsl. Modern environmental conditions in the study area correspond to a sub-humid temperate climate. The mean annual temperature is 13 °C with an annual rainfall of 838 mm (García 1988). The natural vegetation consists of a mixed-forest with *Pinus oaxacana*, *Quercus crassipes*, *Quercus castanea*, *Quercus dentalis*, and *Arbutus glandosa* in less disturbed areas (Klink 1973). Soils recorded in the region are Lithosols, Regosols, Cambisols, Xerosols, Luvisols, Antroposols and Andosols (according to FAO soil classification – legend of the UNESCO Soil Map of the World, 1974 in Werner et al. 1978).

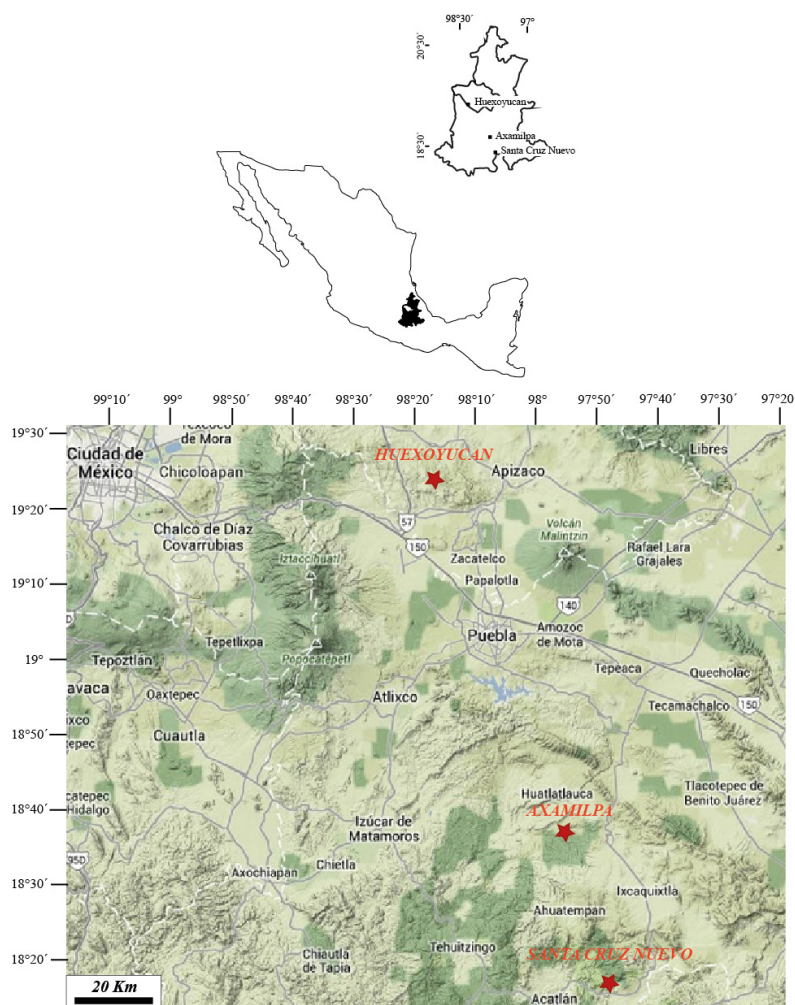


Figure 1. Location of the study areas: Huexoyucan, in the state of Tlaxcala, and Axamilpa and Santa Cruz Nuevo, in the state of Puebla. The state limits are marked with discontinuous white lines.

The other two areas belong to the High Balsas Basin in the south of the state of Puebla. The Axamilpa study area is close to the river Axamilpa in the town of Tepexi de Rodríguez at 18°36'49''N, 97°54'45''W, at around 1608 mamsl; while Santa Cruz Nuevo is closed to the Acatlán river in the town of Totoltepec de Guerrero at 18°18.68'N y 97°48.63'W, around 1520 mamsl. Both areas belong to the physiographic province of Eje Neovolcánico, particularly to the subprovince Sur de Puebla characterized by a sub-humid warm climate (Fernández-Nava et al. 1998). The areas of Axamilpa and Santa Cruz Nuevo are close to the Tehuacan-Cuicatlan Biosphere Reserve and present xeric shrublands with a dominance of cacti, magueys and other succulent plants. The modern soils are Calcareous Phaeozems and Cambisols respectively, according to the criteria of WRB (2006).

All three sites present similar geological settings: high gradational river terraces with elevations 15 to 30 meters above the present river bed. Alluvial sediments in Huexoyucan consist mostly of the volcanogenic minerals derived from andesitic tephros of La Malinche and local monogenetic volcanoes. For the two sites south of Puebla, the main sources for fluvial sediments are andesitic tuffs, lacustrine travertines and Mesozoic limestones in Axamilpa; while in Santa Cruz Nuevo the sources for sediments are the Jurassic sandstones and the Paleozoic gabbro.

Fossil megafauna remains have been reported in the three localities. In Huexoyucan, the fauna discovers consist of canines and flat bones of mastodons, glyptodont plates, molars and teeth of horses, and bison remains (Martínez et al. 2005). In the Axamilpa valley, remains of mastodons (*Cuvieronius tropicus*), edentates (*Glossotherium (Paramylodon)* sp.), horses (*Equus* sp.), mammoths (*Mammuthus* cf. *M. columbi*), giant armadillos (*Glyptotherium* sp.), bison (*Bison* sp.) and llamas (*Paleolama* sp.) (Torres-Martínez and Agenbroad 1991; Montellano-Ballesteros 2002) have been found.

In Santa Cruz Nuevo, the megafauna remains correspond to deer (*Odocoileus* sp.), giant

armadillos (*Pampatherium mexicanum* and *Glyptotherium* sp.), horses (*Equus conversidens*), mammoths (*Mammuthus* sp.), and unidentified genera of deer, bears, goats and mastodons (Tovar et al. 2007).

For the three localities, the physical and chemical analyses of the different paleopedological units follow Birkeland (1999). Soils were described according the criteria of World Reference Base for Soil Resources (WRB 2006) and Retallack (1990).

The Huexoyucan sequence, around 15 m deep, and the Axamilpa sequence, around 21 m deep, were described and sampled in single outcrops, while the approximately 27 m deep Santa Cruz Nuevo sequence was studied in four outcrops from which a compound stratigraphic profile was built up. The chronostratigraphic profiles of the studied soil-sedimentary sequences are presented in Figure 2. The paleopedological units selected for micromorphological analysis are marked with grey rectangles.

Samples were taken from these selected horizons for the preparation of thin sections. Thin-sections (30 μ m thick) were prepared from undisturbed soil samples impregnated at room temperature with the resin Cristal MC-40, studied under a petrographic microscope and described following the terminology of Bullock et al. (1985). The study was focused on the micromorphological characteristics indicative of pedogenetic processes (especially microstructure, porosity, pedofeatures) and types of sedimentary processes and environments (microlamination, microfossils, etc.). Twenty-seven thin sections were analyzed (11 from Huexoyucan, 9 from Santa Cruz Nuevo and 7 from Axamilpa).

In the course of microscopic study of thin sections, abundant opaline microfossils were observed in some paleosol units, promising an additional microscopic paleoenvironmental proxy. We extracted the biogenic opaline particles from horizons 16A and 2A in the Axamilpa sequence through the method of Madella et al. (1998). Samples were mounted

on the slides with glycerin and 200 forms of silica bodies were counted under a petrographic microscope.

Pollen extractions also were made in horizons 6Agh and 6AC following the standard palynological technique. The pollen identification was made under an Olympus BX50 microscope recognizing the number and type of apertures, ornamentation, size, grain form and structures. In the same horizons, diatom species were identified according to the manuals of Kramer and Lange-Bertalot (1991) and the samples

were prepared though the technique of Patrick and Reimer (1966, 1975).

The $\delta^{13}\text{C}$ was obtained from organic matter in paleosols and sent to Laboratorio Universitario de Geoquímica Isotópica (LUGIS), UNAM. The radiocarbon age estimation of humus samples was carried out in the Beta Analytics laboratory and AMS dated. Calibrate dates were obtained through <http://www.calpal-online.de/index.html>. The results of physical, chemical and isotopic analyses are published in Solís-Castillo et al. (2012) and Tovar et al. (2014).

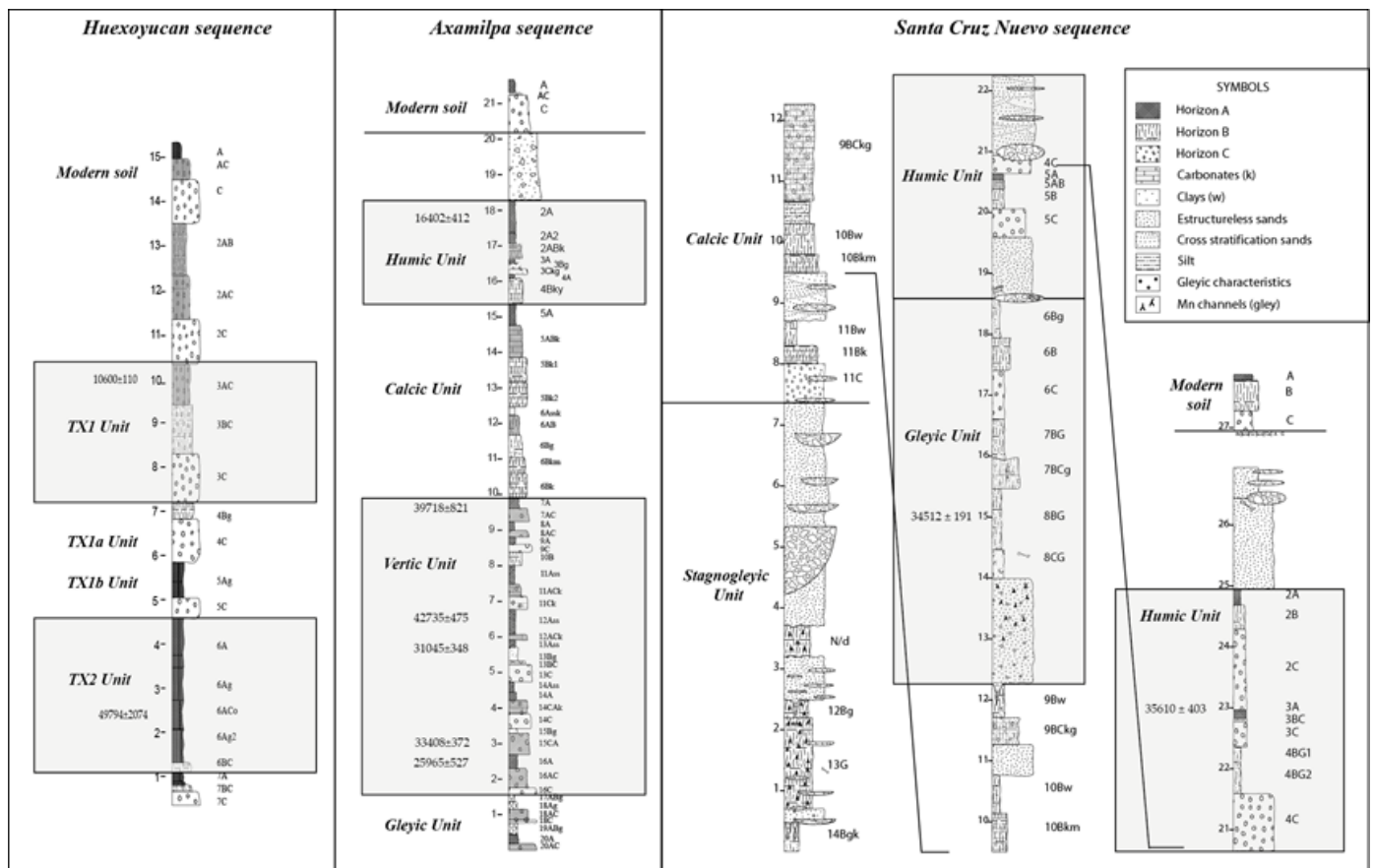


Figure 2. Stratigraphic schemes of the Huexoyucan, Axamilpa and Santa Cruz Nuevo paleosol sedimentary sequences. The gray square indicates de pedological units analyzed in this study.

3. Results

3.1. Morphology, age and selected analytical characteristics of the dark alluvial soils

The three sequences correspond to floodplain deposits and in the three we found similarities in their dark horizons as in the low content of organic carbon, except in TX2 (Table 1). However some differences exist in their texture. In fact, there are important differences between

horizons in the same unit as evidenced by the standard deviation (Table 1, the standard deviation is presented as σ).

The sediments of Axamilpa are mainly fines, corresponding to clay/mud, while Santa Cruz Nuevo sequence has a larger proportion of clay and silt.

Table 1. Content of organic carbon and texture of the studied paleosols of Axamilpa, Santa Cruz Nuevo, Huexoyucan. The values are the average of all horizons in each unit

	Axamilpa		Santa Cruz Nuevo		Huexoyucan	
	Vertic Unit	Humic Unit	Gleyic Unit	Humic Unit	TX1	TX2
Number of samples	25	8	11	14	4	9
% Organic carbon	0.54	0.41	0.46	0.54	0.34	1.61
σ	0.49	0.12	0.48	0.33	0.21	1.86
% Clay	61.13	60.06	33.45	35.15	21.97	44.11
σ	15.35	13.09	24.18	21.46	14.60	23.57
% Silt	24.47	29.91	43.87	46.47	22.01	25.14
σ	11.11	13.48	23.33	23.63	12.47	11.35
% Sand	14.40	10.04	22.68	18.38	56.05	30.74
σ	15.29	3.91	16.54	9.58	25.73	23.12

The TX2 unit of Huexoyucan constitutes a pedocomplex with three paleosols (Figure 2) classified as Histic Fluvisols (Solís-Castillo et al. 2012). The 6A horizon shows accumulation of dark humus, clay and detrital organic matter, while 6Ag has strong redoximorphic features with a series of iron oxide laminations following the slope orientation. Very high clay content variations from 16% to 88% reflect control by fluvial sedimentation processes rather than pedogenic clay accumulation. The total organic carbon (TOC) values are low (< 1%), however in 6Ag and 6ACo horizons we find the maximum concentration (5%) among all studied paleosols. TX1 is constituted by two paleosols classified as Fluvisols. Paleosols are characterized by

the accumulation of dark humus, particularly in biopores, developing a biogenic porosity and a subangular blocky to granular structure.

The Vertic Unit of Axamilpa is comprised of ten clayey paleosols with slickensides and coarse angular blocky structures (Figure 3A). Imbricated pebbles are found in some horizons. Yellow patches are common in all horizons.

The Humic Unit of the same pedosequence (Figure 3B) is comprised of three paleosols. The structure varies between blocky and granular with Ah dark horizons. The Ah horizons are deeper than in the previous unit. Also, some horizons have gleyic characteristics present as

yellow-brown patches. Under this Unit, fossils of *Equus* sp., *Mammuthus* cf., *M. columbi* and *Glyptotherium* sp. have been found.

In Santa Cruz Nuevo there is more evidence of active channels associated with paleosols. In this area paleosols are less developed than in the other two and the sand content is higher. The Gleyic Unit is 459 cm high and is consists of three paleosols and one pedosediment corresponding to redeposited paleosols. The

pedosediment has a green-gray color with some yellow patches, a large proportion of clay (around 40%), and no pedogenic structure. Pebbles and Mn dendrites are found. The content of clay in gleyic paleosols is around 10%. The gleyic paleosols have an angular blocky structure with many yellow-brown patches and few channels filled with Mn (Figure 3C). In the gleyic sediments fossil megafaunal remains of *Glyptotherium* sp., *Ursidae*, *Equus conversidens* and *Mammuthus* sp. have been found.

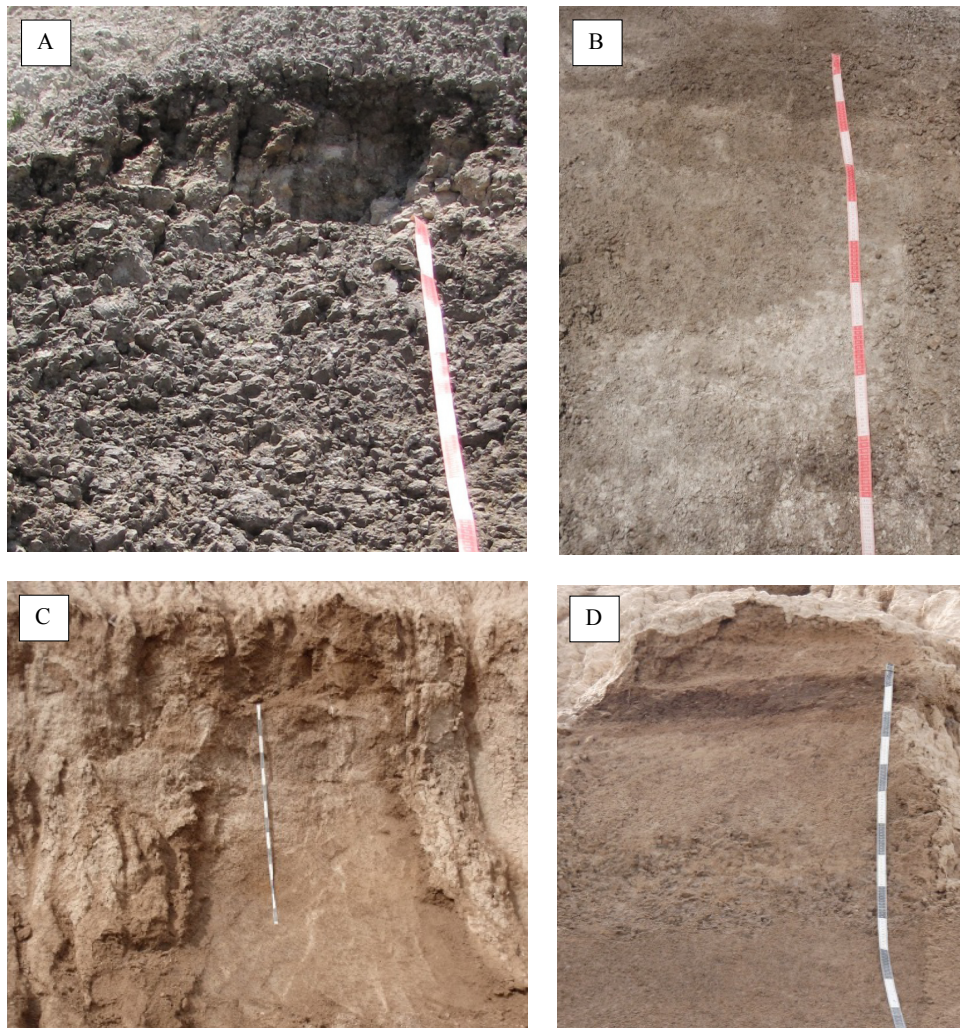


Figure 3. The views of the four pedostratigraphic units analyzed in this study. **A.** The Vertic Unit of Axamilpa. **B.** The Humic Unit of Axamilpa. **C.** The Gleyic Unit of Santa Cruz Nuevo. **D.** The Humic Unit of Santa Cruz Nuevo.

The Humic Unit of Santa Cruz Nuevo consists of four paleosols and is thicker (785 cm) than in Axamilpa (292 cm). The Ah horizons of Santa Cruz Nuevo are shallower than those of Axamilpa, however, they have a darker color and better pedogenic structure, which is granular (Figure 3D). The texture is mainly silt-sandy and in the Ah horizons there are remains of charcoal. In the upper paleosols, there is evidence of sedimentary lenses and lamination. In the Humic Unit the

megafauna fossils are *Glyptotherium* sp., and *Odocoileus* sp.

The time span covered by the three localities is from the end of marine isotopic stage 3 (MIS3) to the early Holocene (EH). The localities of Huexoyucan and Axamilpa correspond to the end of MIS3 and MIS2. Huexoyucan also covered the Holocene while Santa Cruz Nuevo only covered MIS3. Table 2 shows the radiocarbon values of humus samples and the $\delta^{13}\text{C}$.

Table 2. Radiocarbon ages of paleosol humus of selected horizons in the three localities

	Radiocarbon ages AP	Calibrated ages AP ¹	$\delta^{13}\text{C}$
Huexoyucan			
TX2			
6 ACo	46 320 ± 870 (Beta-250975)	49 724 ± 2074	-26.5
TX1			
3AC	9 260 ± 50 (Beta-250974)	10 426 ± 88	-18.8
Santa Cruz Nuevo			
<i>Humic Unit</i>			
3A	31 680 ± 120 (Beta-277570)	35 610 ± 403	-19.5
<i>Gleyic Unit</i>			
8Bg	30 380 ± 220 (Beta-277569)	34 512 ± 191	-22.5
Axamilpa			
<i>Vertic Unit</i>			
7A	34 350 ± 270 (Beta-300438)	39 718 ± 821	-22.1
12 Ass	38 310 ± 320 (Beta-300439)	42 735 ± 475	-23.4
13Ass	26 140 ± 170 (Beta-277567)	31 045 ± 348	-21.9
15CA ²	28 900 ± 220 (Beta-261618)	33 408 ± 372	-22.5
16 A	21720 ± 40 (Beta-261619)	25965 ± 527	-23.3
<i>Humic Unit</i>			
2A	13 450 ± 60 (Beta-261620)	16 402 ± 412	-23.91

¹ Calibrated according to CALPAL online: <http://www.calpal-online.de/index.html>.

² Charcoal sample.

3.2. Micromorphological observations

The matrix of the dark humus horizon of TX2 includes laminated organic material and rounded rock fragments stained with Fe and Mn oxides (Figure 4B). Dark reddish clay infillings are dense and fractured (Figure 4C). In the gleyic horizon at base of the profile, the color of the matrix is

reddish, with ferruginous mottles. Weathering of volcanic minerals and rock fragments resulted in their fracturing and partial substitution with yellow clay (Figure 4D). We observed abundant opaline microfossils - sponge spicules, diatoms and phytoliths, which are incorporated into the matrix (Figure 4A; Tables 3 and 4).

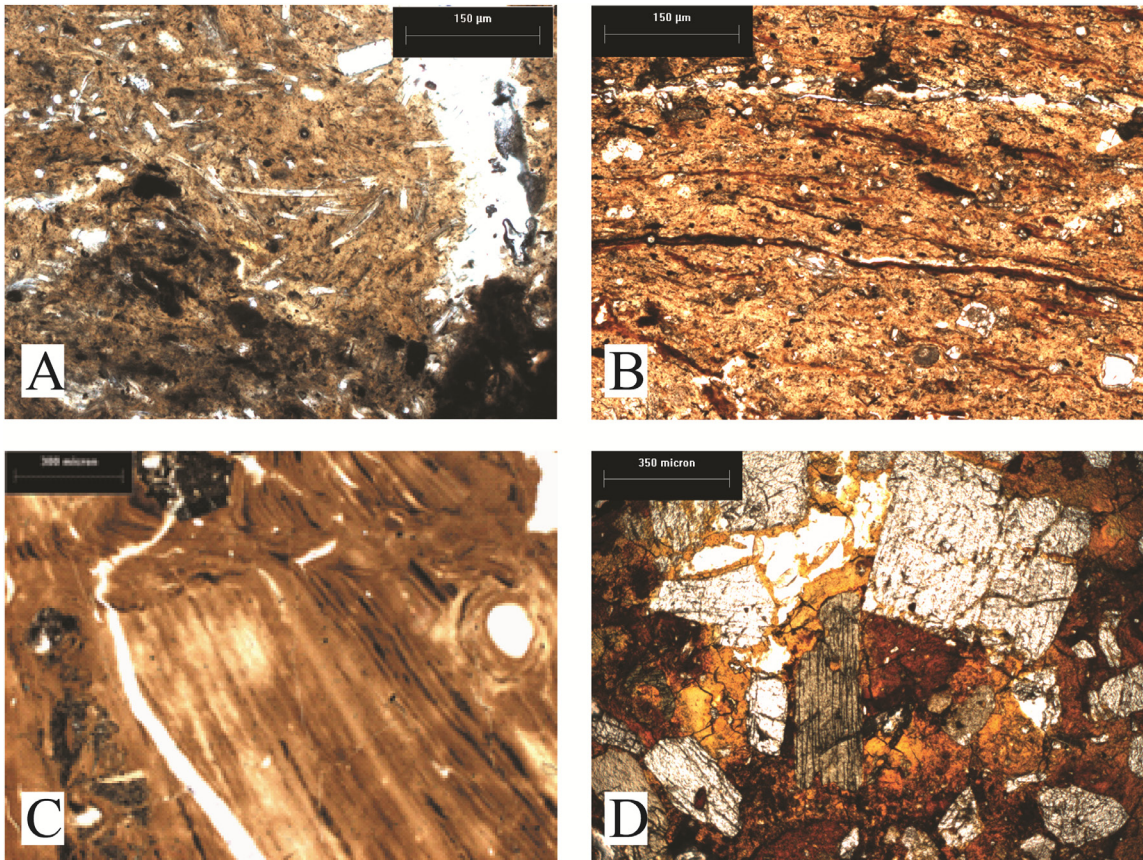


Figure 4. The micromorphology of the TX2 humus horizon, Huexoyucan section. **A.** Silica microfossils in the groundmass, PPL. **B.** Sedimentary microlamination, PPL. **C.** Microlaminated clay infilling, PPL. **D.** Weathered rock fragment, yellow clay fills the spaces between primary mineral grains and penetrates their fractures. PPL.

Table 3. Opaline microfossils and pollen data from studied areas

	Vertic Unit	Humic Unit	TX2
C3 grasses	19.4%	48.0%	4%
C4 grasses	32.4%	19.7%	-
Conifers	7.2%	5.0%	15.3%
Other C3 plants	7.7%	8.4%	-
Other C4 plants	-	-	11.9%
CAM plants	-	-	1.1%
Algae (Diatoms)	24.7%	14.4%	36.5%
Other kind of Algae	-	-	10.8%
Sponge spicules	5.4%	2%	19%
Non diagnostic forms	3.2%	2.5%	1.46%

Table 4. Genera and species of diatoms of TX2 in Huexoyucan

Navicula sp.	2.96%
Hantzschia sp.	3.62%
Gomphonema sp.	6.58%
Cymbella sp.	8.55%
Aulacoseira sp.	12.83%
Epithemia turgida	2.63%
Epithemia sp.	7.89%
Eunotia papilo	2.63%
Eunotia sp.	9.21%
Crysophyta	4.93%
Pinnularia sp.	3.95%
Sponge spicules	34.21%

The micromorphology of the TX1 basal horizon shows partially decomposed plant tissues. The horizon is compact, no clear pedality is visible, and pore space consists of few disconnected fissures and channels. Most of the primary minerals are weathered, however some are fresh, such as volcanic glass; the minerals have clay and organic coatings; very few clay coatings are limpid and laminated. In the 3AC horizon of the TX1 paleosol, the amount of organic matter decreases and is represented mostly by colloidal organic pigment; numerous granular excremental aggregates are separated by biopores that are partly filled with illuvial clay. The coatings are microlaminated. The 3C horizon shows a more compact structure that is

laminated and fissured. Volcanogenic minerals of the coarse fractions are slightly weathered.

In the Axamilpa profile, the micromorphology demonstrated differences between the two units. The Vertic Unit has a microsparitic carbonate matrix with a blocky structure. There are many fractures, consequences of compression (Figures 5A and 5D). Conspicuously strong fracturing disturbs but does not destroy the primary sedimentary lamination (Figure 5A). There are some calcite hypocoatings around pores (Figures 5B and 5E). As discussed in Tovar et al. (2014), some of these calcite hypocoatings could be the consequence of algae precipitates. They are associated with lacustrine fauna

such as diatoms and mollusks (bivalves and gastropods) (Figures 5B and 5C).

Thin sections of the Humic Unit of Axamilpa have a groundmass consisting of micrite, clay and humus pigment. Some microareas show strong development of a coprogenic granular structure with high porosity, whereas others are more compact with blocky pedality formed by fissures (Figures 5F and 5G). There are many biogenic channels, chambers and voids (Figure 5F). The

weathering grade of most crystalline silicates is low; however a few pumice fragments are completely substituted by clay due to pedogenic alteration. Redoximorphic features are few, presented by ferruginous nodules and very thin coatings (Figures 5I and 5J). Opaline microfossils associated with these units are presented in Table 3. The most abundant and most complete forms of silica bodies are in the Vertic unit. In the Humic unit, these are fragmentary and scarce.

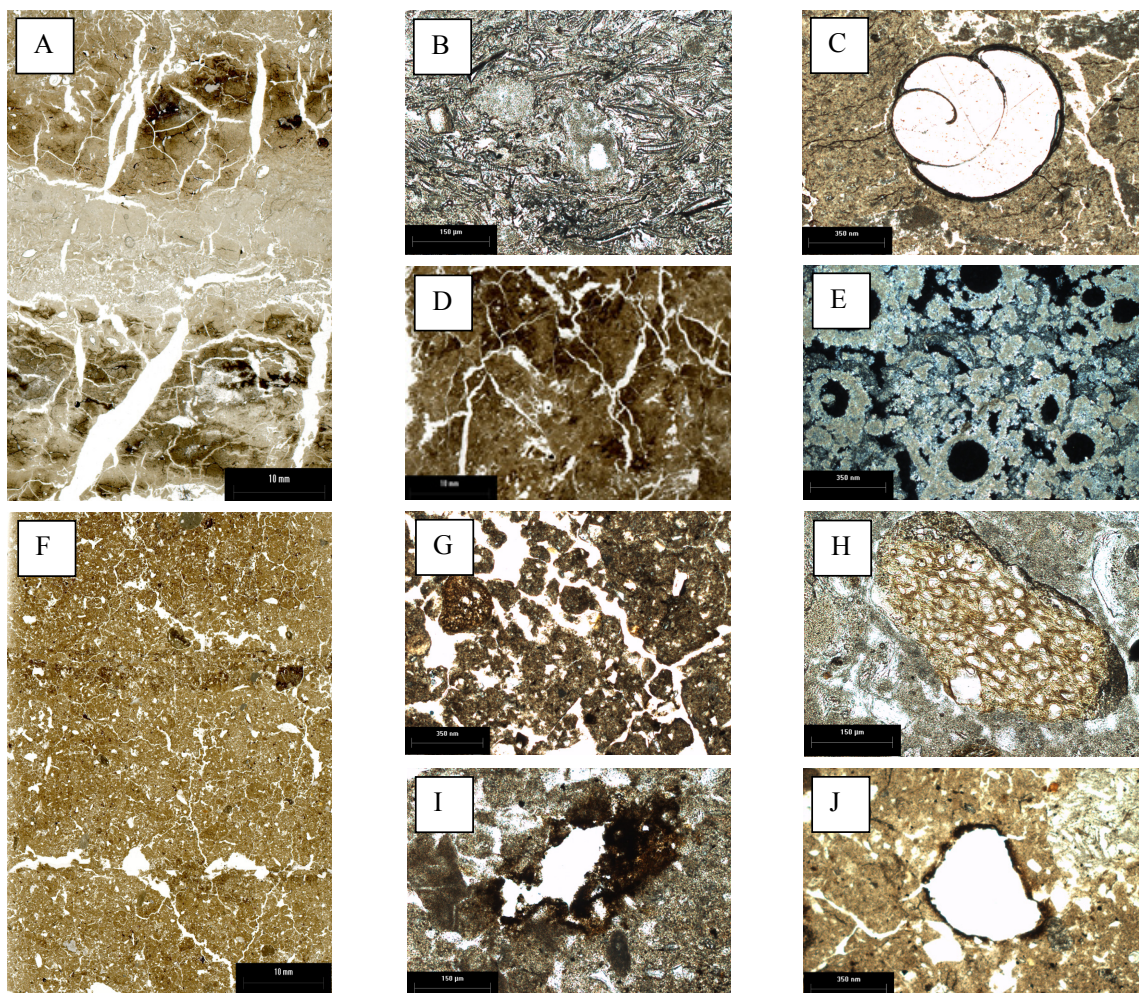


Figure 5. The micromorphology of Axamilpa. A-E correspond to the Vertic Unit. **A.** Scanned thin section of the 12ACK paleosol of the Vertic Unit showing sedimentary lamination and fracturing. **B.** Diatoms, PPL. **C.** Gastropod valve, PPL. **D.** Thin section of the paleosol 13Ass of the Vertic Unit with their fractures caused by contraction, PPL. **E.** Microsparitic hypocochings of the paleosol, probably caused related to algae biomineralization. F-J correspond to Humic Unit. **F.** Scanned thin section of the paleosol 2A. Note frequent pores. **G.** Coprogenic granular structure (left) with some blocks (right). PPL. **H.** weathered pumice fragment, PPL. **I.** and **J.** Ferruginous redoximorphic pedofeatures, PPL.

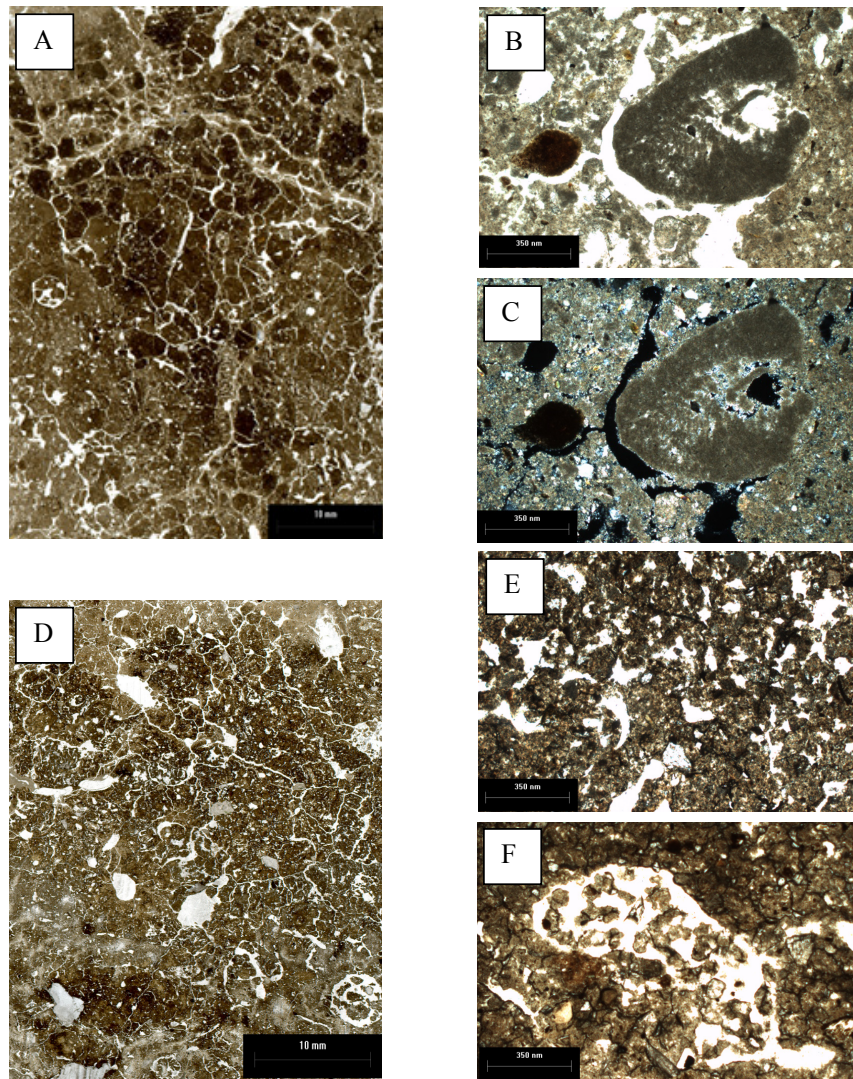


Figure 6. The micromorphology of Santa Cruz Nuevo. A-C correspond to Gleyic Unit. **A.** Scanned thin section of the 6Bg paleosol of the Gleyic Unit: compact arrangement, pores – predominantly thin fissures. **B.** Small ferruginous (left) and large micritic (right) nodules, PPL. **C.** Same as B, note the interference colours of the micritic nodule and dark colour of the ferruginous nodule. D-F correspond to Humic Unit. **D.** Scanned thin section of the paleosol 5A with many pores and chambers. **E.** Partly welded granular aggregates forming spongy fabric. **F.** Infilling of coprogenic aggregates in a pore.

In the Santa Cruz Nuevo exposure, thin sections of the Gleyic Unit paleosols show a compact structure of subangular or rounded blocks formed by a net of fractures (Figure 6A). The groundmass of the paleosols of the Gleyic Unit is dominated by micritic and microsparitic carbonates. The pedofeatures are represented by few impregnative ferruginous nodules and more frequent compact micritic nodules (Figure 6B). Frequent black mottles in a dendritic pattern (Mn hydroxides) are formed over blocks.

The most developed paleosols in Santa Cruz Nuevo are found in the Humic Unit. Their groundmass is strongly pigmented with dark humus; biogenic channels, chambers and voids are more frequent (Figure 6D). Although a compact blocky structure is dominant, some microareas are dominated by partly welded granular aggregates forming a spongy fabric (Figure 6E). Chambers with loose excremental infillings are evidence of mesofauna activity (Figure 6F). Redoximorphic features are few. No opaline microfossils were found.

4. Discussion

4.1. Micromorphology and paleoenvironmental inferences

The radiocarbon dates of dark alluvial soils support the hypothesis that the two main intervals of their formation occurred within the Late Quaternary: the second half of MIS3 and the end of MIS2 (Late Glacial) and adjacent Pleistocene-Holocene transition. The set of features observed in the oldest paleosols of Huexoyucan, Santa Cruz Nuevo and Axamilpa developed during MIS3 reflect the influence of sedimentation and pedogenesis under aquatic conditions.

In Huexoyucan, the Histic Fluvisol (TX2) shows microlamination, incomplete decomposition of organic matter and abundant microfossils of aquatic organisms, which point to a hydromorphic synsedimentary pedogenesis. The accumulation of dark humus that impregnates the soil matrix is not accompanied by the development of biogenic structure and porosity, thus supposing its hydromorphic origin in a swampy landscape. The latter is also confirmed by abundant redoximorphic features at the base of the TX2 profile. Shorter periods of better drainage are indicated by evidence of clay illuviation and moderate silicate weathering.

The diatom record (Table 4) supports the hypothesis of wetland pedogenesis for TX2, and allows precise determination of the particular characteristics of the wetland ecosystem. The presence of *Eunotia*, *Ephitemia*, *Cymbella*, *Gomphonema*, *Hantzschia*, *Crysophyta* and *Melosira* (*Aulacosiera*) indicates the existence of shallow bodies of cold water (5-12 °C) with low mineralization indicative of oligomesotrophic conditions. Genera *Pinnularia*, *Eunotia* and *Melosira* can tolerate desiccation and reflect shallow water; however, the abundance of sponge spicules indicates significant fluctuations. The diatom species suggest a marked seasonality (increase of water level during wet periods and slightly turbid water in dry seasons), and are associated with cold environments.

Similarly, the microscopic analysis of the Vertic Unit of Axamilpa revealed a laminated deposit

with the presence of aquatic fossils (diatoms and mollusks; Figures 5B and 5C) as well as hydrogenic accumulation of carbonates (algae biomineralization; Figure 5E). All these features point to synsedimentary soil development in an ancient marsh. The microlaminations are overprinted by fractures that were produced by expansion-contraction of vertic soils. Vertic soils are indicative of a seasonal climate with distinct annual wet and dry seasons. Vertic soils commonly developed over alluvial material in flat areas in a wide range of ecosystems (Wilding et al. 1983). In the particular case of the Axamilpa section we observe that the fracturing and development of blocky structure overprints, but does not completely destroy the original sedimentary lamination. We conclude that the Vertic processes occurred during rather short periods of improved drainage and soil drying.

The analysis of opaline microfossils provides complementary evidence for understanding environmental evolution during the Vertic unit development. Opaline microfossil counts (Table 3) reveal an abundance of plants, particularly grasses, over aquatic forms (mainly diatoms and some sponge spicules). We suppose that this contrasting microfossil association could be linked to the multiphase pedogenesis indicated by micromorphological observations. Aquatic microfossils are probably associated with the initial synsedimentary marshland phase, whereas grass phytoliths (especially those of C4 type) correspond to the late dry Vertic stage.

The presence of channels and cross-stratification in the sediments of Santa Cruz Nuevo is evidence of important fluvial activity. The green pale colors of the sediments at the base of Gleyic Unit and the absence of mesofaunal activity support the idea of aquatic conditions. The presence of ferruginous nodules and hydrogenic micritic pedofeatures also indicate hydromorphic pedogenesis. However, manganese mottles are more abundant than blocky aggregates, which suggests that hydromorphism was not very strong because Mn is rather easily mobilized by redoximorphic processes (Gerrard 1992; Schaetzl and Anderson 2005). The overlying Humic unit of Santa Cruz Nuevo, also formed

during MIS3, shows certain tendencies towards better-drained pedogenic conditions. At a micromorphological level, the presence of root channels and pores with evidence of the digestive activity of mesofauna are evidence of better aeration.

The paleosols formed at the end of MIS2 – transition to the Holocene generally demonstrate the features of soil formation in a better-drained environment, supporting development of a structured, porous Ah horizon.

The Humic Unit of Axamilpa, corresponding to the end of MIS2, is characterized by the absence of sedimentary features and the presence of microchannels and voids produced by roots and mesofauna; redoximorphic features are few and poorly developed. All these indicate an advanced pedogenesis in a stable, moderately drained meadow landscape. However, the opaline microfossil count indicates the presence of diatoms that are present in a minor proportion and are fragmentary. The abundance of grasses suggests that a grassland ecosystem predominated the area during this time.

The upper humic paleosol of Huexoyucan, TX1, corresponds to the Pleistocene-Holocene transition period and shows somewhat different features to the TX2 wetland paleosol corresponding to MIS3. The strong biogenic structure reflects pedogenesis occurring under good soil drainage conditions and sufficient aeration. Also, evidence of clay illuviation points to a free drainage that afforded percolation of suspensions. However the increased thickness of the Ah horizon points to high sedimentation rates during this period. Borejsza and Frederick (2010) discussed the activation processes causing landscape instability with an increase in the discharge of rivers and alluvial sedimentation. Such conditions are the result of the transition from glacial to interglacial conditions as reported by Heine (1994).

We conclude that the “younger” humus paleosols of the Late Quaternary alluvial sequences were formed under moderately drained conditions of moist floodplain meadows. In general, wetlands

and moist meadows of the alluvial geosystems could be an important element of the megafauna subsistence during the Late Pleistocene.

4.2. Correlation of paleoecological records: towards understanding the megafauna ecosystems during MIS3-MIS2

In all studied sequences we had an opportunity to compare the paleoecological inferences from the microscopic studies of the soil thin sections and opaline microfossil extracts with other records from the same profiles: stable carbon isotopes of humus, palynological spectra and the remains of paleofauna.

The Histic Fluvisol of Huexoyucan and the Vertic Unit of Axamilpa share similar characteristics in their stable isotope signatures and vegetation records. In Huexoyucan, the $\delta^{13}\text{C}$ composition shows a minimum of -26.5‰, with values fluctuating up to -18.8‰, which are associated with dominance of C3 vegetation (Lounejeva-Baturina et al. 2006). Palynological analysis of the organic horizons of TX2 showed the presence of a forest ecosystem (*Pinus*, *Alnus* and *Quercus*) coexisting with amaranth (Chenopodiaceae-Amaranthaceae), grasses (Poaceae), and Cyperaceae (Solís-Castillo et al. 2012).

In the Vertic Unit, the values of $\delta^{13}\text{C}$ (-23.4 to -21.9) and the phytolith record (Table 3) are evidence for the coexistence of C3 and C4 plants in a similar proportion. However the $\delta^{13}\text{C}$ values suggest that C3 plants dominated the area.

In Santa Cruz Nuevo, the Gleyic and Humic Units belong to MIS3; however their stable isotope signatures differ. The lower topographic unit is the Gleyic. Although gleysols are found in low topographic reliefs in almost all climates (WRB 2006), the $\delta^{13}\text{C}$ value of -22.5 indicates C3 vegetation during MIS3. The presence of *Equus conversidens* and *Mammuthus* sp. suggests grassland (Hibbard and Taylor 1960; Agenbroad 1984); while giant armadillos (genus *Glyptotherium*) have been suggested in areas with tropical to temperate climates, feeding on leaves along the water bodies (Gillette and Ray 1981).

All these paleocological proxies from the MIS3 paleosol units agree with their interpretation as wetland synsedimentary soil bodies inferred from microscopic studies. We suppose that under the more humid paleoclimate of MIS3, wetland ecosystems were much more widespread than at present, and the corresponding soil types played important role in the soil mantle of that period. Within Tlaxcala Block at the higher landscape positions (altitude around 2550 m, 70 m elevation difference), other paleosols belonging to the TX2 pedomorphological level and thus synchronous with the MIS3 Histosol of Huexoyucan have been described (Sedov et al. 2009; Solís-Castillo et al. 2012). Most of these upland TX2 paleosols belong to Luvisols, which also reflect humid paleoclimatic conditions.

The Humic Unit of Santa Cruz Nuevo has more a positive stable carbon signature, with a $\delta^{13}\text{C}$ value of -19.5, indicating the contribution of C4 vegetation. The megafauna fossils recovered from this Unit correspond to *Glyptotherium* sp., and *Odocoileus* sp. Deer inhabit a great variety of habitats including temperate pine forest, oak woodlands, oyamel forest and shrublands (Ceballos-González and Galindo-Leal 1984). Because the $\delta^{13}\text{C}$ values are similar to the present values (-18.46) the area probably was shrubland as it is now.

During MIS2, the environmental conditions were cool as evidenced by the Humic Unit of Axamilpa, and although the $\delta^{13}\text{C}$ value is maintained (-23.91), there is an important increment of C3 grasses (Table 3) supporting the idea of a C3 grassland. This scenario is in accordance with other studies in which fossil horses (*Equus* sp.) and mammoths (*Mammuthus* cf. *M. columbi*) were found (Hibbard and Taylor 1960; Agenbroad 1984). During the Pleistocene-Holocene transition, the climate must have become warmer as evidenced by more positive $\delta^{13}\text{C}$ values in TX1 (-18.8‰). All these data agree with the hypothesis of meadow pedogenesis for these units, inferred from microscopic observations.

At a global scale, the extensive research done in temperate zones registers the dominance of

cold dry climates, during the MIS2, allowing loess sedimentation and limiting soil development (e.g. Bronger et al. 1998). However in Central Mexico, Sedov et al. 2001 document the presence of well-developed paleosols in Nevado de Toluca for the period MIS3-MIS2 which evidence more humid conditions. The three study pedosequences: Huexoyucan, Santa Cruz Nuevo and Axamilpa are also in good agreement with an interpretation of humid paleoenvironments. Nevertheless, research on lacustrine basins in Central Mexico shows strong differences. For instance, Lozano-García et al. 1993, Lozano-García and Xelhuantzi (1997), and Caballero et al. (1999) report low lake levels related to drier conditions during Last Glacial Maximum and Late Glacial. We suggest that our data depicting a change from hydromorphic wetland pedogenesis during MIS3 to better-drained meadow soils during MIS2 may reflect the trend to dryer paleoclimatic conditions since MIS3. Also, the phytolith record indicates a decrease in forest forms and an increase in grasses. The tendency for decreasing forest forms close to LGM has been inferred by other workers in lacustrine sediments in the Central Mexican Highlands (e.g. Lozano-García et al. 2005).

5. Conclusions

The micromorphological comparison of the three sequences indicated that they shared similar processes and characteristics. During MIS3, all areas presented hydromorphic conditions such as microlamination and oxides as evidence for synsedimentary characteristics. In Huexoyucan and Axamilpa there are also microfossils of diatoms and sponges which occurred in a cool environment according to the isotopic values. Similar isotopic values are found in the Humic unit of Axamilpa, corresponding to MIS2, however we observed developed paleosols without evidence of sedimentation and with a major proportion of grasses. During the transition to Holocene, we observed a trend to

more positive $\delta^{13}\text{C}$ values, indicating warmer conditions. Even with this trend, all sequences correspond to humid pedogenesis, particularly during MIS3. The major findings of megafauna in the studied areas were in Santa Cruz Nuevo and correspond to this stage. Fossil findings can be associated with a minor development of paleosols preventing the incorporation of the bones to the carbon cycle. Also, the presence of water bodies suggests abundant vegetation that is considered to be an important factor for allowing the development of megafauna that lived in this region. The micromorphology does not give many clues about ecosystems however, the reported ecological requirements of the extinct fauna suggested that the fauna probably inhabited C3 grasslands/shrubland.

According to our results, past conditions were different from those found in the Holocene, in which the climatic conditions got dryer.

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Discusión

Reconstrucción de los paisajes presentes en Santa Cruz Nuevo y Axamilpa

El estudio de las localidades de Santa Cruz Nuevo y Axamilpa permitió la reconstrucción de las condiciones locales reinantes durante el final de la MIS 3 a la MIS 2.

Debido a las probables condiciones ambientales al momento del depósito, las características sedimentarias, pedológicas y bióticas son contrastantes en ambas localidades (Figura 5 y Cuadro 4).

Del depósito de Santa Cruz Nuevo fueron tomadas 2 muestras de humus que sitúan a la localidad alrededor de los 30,000 ¹⁴C años, finales de la MIS 3.

Los depósitos sedimentarios son de gran espesor y los paleosuelos están pobremente diferenciados permitiendo que en algunos de ellos todavía se observen lentes de grava. La cantidad de arena es significativa en todos los horizontes (alrededor de 20-30%) mientras que la cantidad de arcilla es muy variable entre ellos. Los pocos horizontes A preservados son muy someros. El análisis micromorfológico soporta la conclusión de que se trata de paleosuelos incipientes con cantidades variables de óxidos de Mn y Fe. Existen evidencias variables de actividad biológica.

La fauna fósil recuperada corresponde tanto a megafauna (*Odocoileus* sp., *Pamphatherium mexicanum*, *Glyptotherium* sp., *Equus conversidens*, *Mammuthus* sp., y géneros no identificados de venado, oso, cabra y mastodonte) como microvertebrados (*Ambystoma* sp., *Bufo occidentalis*, *Bufo* cf. *B. valliceps*, *Bufo* sp., *Rana* sp., *Kinosternon* sp., *Rhinoclemys* sp., *Gopherus* cf. *G. berlandieri*, *Sceloporus* cf. *S. grammicus*, *Sceloporus* cf. *S. horridus*, *Conopsis* sp., *Lampropeltis* sp., *Leptodeira* sp., *Senticolis* sp., *Thamnophis* sp., *Trimorphodon* sp., *Crotalus* sp., restos de Plethodontidae, Scaphiropodidae, Scincidae, *Neotoma mexicana*, *Peromyscus*

difficilis, *Reithrodontomys* sp., *Sylvilagus floridanus*, *Sylvilagus* sp., *Bassariscus* cf. *B. sumichrasti*, *Catharus* sp., *Catharus* cf. *C. occidentalis*, *Callipepla* cf. *C. squamata*, *Cyrtonix* sp.; *Columba fasciata*, *Campylorhynchus* cf. *rufinucha*, *Dumatella* cf. *D. carolinensis*, *Salpinctes* cf. *S. obsoletus*, *Pipilo* sp. y *Icterus* sp.).

Los fósiles se encuentran desarticulados y con escasa evidencia de actividad biológica. Las condiciones que favorecieron la preservación fósil están ligadas a la dinámica de las planicies de inundación. En las planicies de inundación la alta tasa de acreción impide el desarrollo de los suelos. El tener suelos incipientes permite la preservación fósil ya que en los suelos bien desarrollados existe una alta diversidad de microorganismos, principalmente bacterias y hongos, que tienden a degradar los huesos, y las raíces tienden a destruir el tejido esponjoso de las articulaciones de los mismos (Forbes, 2008).

Aunado a lo anterior, se encuentra el pH. El pH juega un papel clave en la preservación ya que aumenta en pH neutros o alcalinos y disminuye en ácidos (Forbes, 2008).

El análisis de los diferentes proxies ambientales indica que el depósito sedimentario de Santa Cruz Nuevo se dio en climas secos. En Santa Cruz Nuevo, el pH debió ser alcalino impidiendo la degradación de los huesos aún de aquellos que son más frágiles como los huesos de las aves además de que no debieron transportarse grandes distancias.

El registro de isótopos estables de carbono en Santa Cruz Nuevo ($\delta^{13}\text{C}$) indica la dominancia de plantas con metabolismo C3 en todas las unidades pedoestratigráficas (Figura 5) con excepción de la Húmica donde se observa una firma mixta.

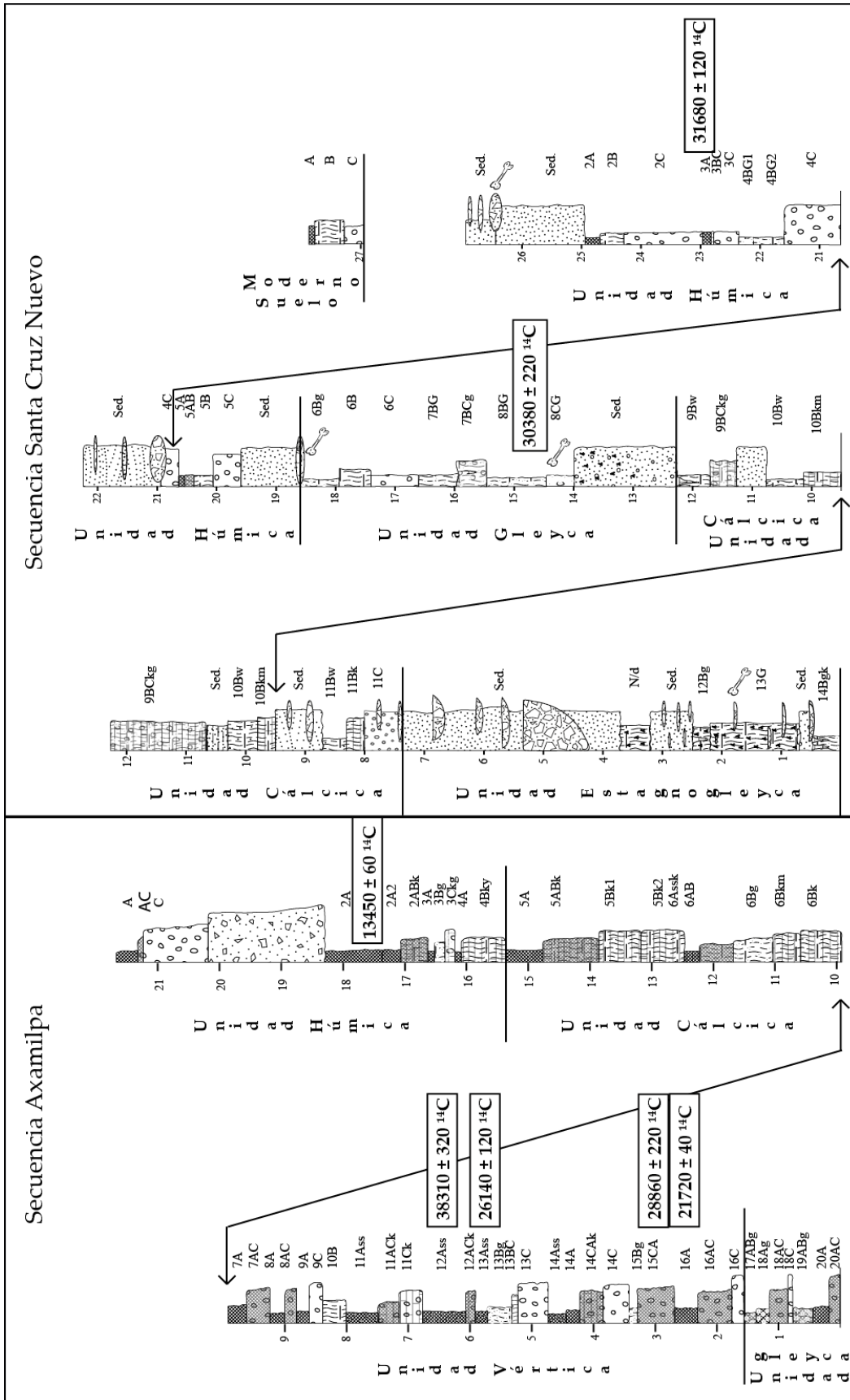


Figura 5. Secuencias pedostratigráficas de las dos secuencias estudiadas.

Cuadro 4. Relación de toda la información presentada en la reconstrucción paleoambiental de las secuencias Axamilpa y Santa Cruz Nuevo.

Localidad	Unidad	Edad de radiocarbono AP	Edades calibradas AP	$\delta^{13}C$	Ecosistema sugerido	Otros proxies utilizados
Axamilpa	Húmica			-23.91 -22.68 -23.48	Pastizal C3	Fitolitos
	Cálcica 2 ^a	13450 ± 60	16402 ± 412	-23.54	Pastizal C3	Fitolitos
	Vértica 7A	34350±270	39718 ± 821	-22.1	Pastizal C4	Fitolitos
	12 Ass	38310±320	42735 ± 475	-23.4		
	13Ass	26140±170	31045 ± 348	-21.9		
	15CA ²	28900±220	33408 ± 372	-22.5		
16 A	21720 ± 40	25965 ± 527	-23.3			
Gleyca			-24.6	Bosque	Fitolitos	
Santa Cruz Nuevo	Húmica 3 ^a	31680±120	35610 ± 403	-19.82 -19.5	Ecosistemas secos	Vertebrados fósiles
	Gleyca 8Bg	30380±220	34512 ± 191	-22.5 -22.3	Ecosistemas secos	Vertebrados fósiles
	Cálcica			-23.22	Pastizal?	Carbonatos
	Estagnogleyca			-23.3 -21.94	Pastizal C3	Vertebrado fósil

La fauna fósil fue recuperada de tres niveles distintos (Unidades estagnogleyca, gleyca y húmica). De la basal, la Unidad estagnogleyca, fueron recuperados restos de *Mammuthus* sp. que por el tipo de dentición se asocia a hábitos pacedores lo cual sería congruente con la firma isotópica que correspondería a pastos C3.

De la Unidad gleyca fueron recuperados restos de salamandras (*Ambystoma* sp., Plethodontidae), sapos (*Incilius* sp. e *Incilius occidentalis*), ranas (*Rana* sp.), sapos pata de pala (Scaphiopodidae), tortugas (*Kinosternon* sp. y *Gopherus* sp. cf. *G. berlandieri*), lagartijas (*Sceloporus* sp. cf. *S. grammicus*, *Sceloporus* sp. cf. *S. horridus*, Scincidae), serpientes (*Conopsis* sp., *Lampropeltis* sp., *Leptodeira* sp., *Senticolis* sp., *Thamnophis* sp., *Trimorphodon* sp., *Crotalus*

sp.), armadillos gigantes (*Glyptotherium* sp.), conejos (*Sylvilagus floridanus*), roedores (*Neotoma mexicana*, *Peromyscus difficilis*, *Reithromomys* sp.), osos (Ursidae), cacomixtles (*Bassariscus* sp. cf. *B. sumichrasti*), caballos (*Equus conversidens*) y mamuts (*Mammuthus* sp.).

De acuerdo a la diversidad faunística de la Unidad gleyca y sus requerimientos ecológicos se infiere que la mayoría de la fauna corresponde a ecosistemas secos (matorral xerófilo y pastizal). Los pastizales están dominados por gramíneas y son frecuentes en las regiones semiáridas y de clima fresco donde la precipitación media anual varía entre 300-600 mm y cuyo pH es cercano a lo neutro (6-8). La textura varía entre migajón arcilloso a migajón arenoso (Rzedowski, 1978).

Por otra parte, los matorrales xerófilos también son característicos de las regiones de clima árido y semiárido con precipitación media anual inferior a los 700 mm y pH entre 6-8.5. Los suelos que sostienen una mayor cantidad de plantas tienden a ser arenosos lo que impide la acumulación de agua. Los matorrales xerófilos no se desarrollan bien en lugares con drenaje deficiente así como suelos francamente salinos, alcalinos y yesosos, mientras que los pastizales sí pueden (Rzedowski, 1978).

La vegetación de los matorrales xerófilos es variada constituida principalmente por cactáceas y crasuláceas donde también hay abundancia de compuestas, gramíneas, leguminosas y agaváceas, entre otras plantas (Rzedowski, 1978).

La evidencia fósil apoya la presencia de un matorral xerófilo con una buena proporción de pastos debido a la presencia de especies pacedoras. Los pastos probablemente tuvieron metabolismo C3 mientras que los constituyentes principales del matorral (cactáceas, agaváceas y crasuláceas) presentan metabolismo CAM, cuyos valores de $\delta^{13}\text{C}$ abarcan tanto los de C3 (-25 a -35 ‰) como los de C4 (-10 a -17‰) dependiendo de la disponibilidad de agua (Edwards y Walker, 1983).

El río probablemente acarrea agua durante todo el año por la presencia de los anfibios haciendo que las plantas que vivían en la ribera del río tuviesen valores de $\delta^{13}\text{C}$ muy negativos.

La presencia de un diente de oso indica la existencia de un ecosistema forestal cercano al área de estudio.

El último nivel fosilífero, la Unidad Húmica, contiene fósiles asignados a sapos (*Incilius sp.*, *Incilius occidentalis*), tortugas (*Kinosternon sp.*), serpientes (*Lampropeltis sp.*, *Thamnophis sp.*, *Crotalus sp.*), aves (*Cyrtonyx sp.*, *Catharus cf. occidentalis*, *Columba fasciata*, *Icterus sp.*, *Pipilo sp.*, *Salpinctes cf. obsoletus*, *Dumetella cf. carolinensis*, *Campylorhynchus cf. rufinucha*, *Callipepla cf. squamata*), armadillos gigantes (*Glyptotherium sp.*), conejos (*Sylvilagus floridanus*), roedores (*Neotoma mexicana*) y venados (*Odocoileus sp.*). En esta Unidad, la mayoría de las especies son habitantes de los matorrales xerófilos lo que sugiere que fue el ecosistema preponderante. Sin embargo, existen elementos de condiciones más húmedas y frías (*Catharus sp. cf. C. occidentalis* y *Columba fasciata*).

Esta inconsistencia en la distribución de la fauna observada en las dos unidades, gleyca y húmica, puede ser producto del transporte. Sin embargo, los huesos de los microvertebrados se quiebran fácilmente, lo que sugiere que el transporte debió ser mínimo por lo que cerca del área de estudio debió existir un bosque.

La figura 6 intenta reconstruir las condiciones reinantes durante la MIS 3 en Santa Cruz Nuevo y compararlas con el Presente. De acuerdo a los ecosistemas reconstruidos, las condiciones ambientales no variaron significativamente.



Durante finales de la MIS 3



Actualmente

Figura 6. Comparación entre los paisajes que dominaron Santa Cruz Nuevo al final de la MIS 3 y en la actualidad.

En las dos ventanas temporales analizadas, a través de los paleosuelos y su memoria edáfica, se sugiere que las condiciones ambientales fueron relativamente secas con predominio de matorrales xerófilos y pastizales, y muy probablemente cerca del área hubo un bosque. La vegetación actual corresponde a un matorral rosétofilo y solo cerca del río Acatlán se desarrolla un bosque de galería.

Existen dos tipos de climas. El clima predominante es el semi-cálido subhúmedo con lluvias en verano A(C)wO(w), cuya temperatura media anual varía entre 22-25 °C; con precipitación pluvial anual de 759 a 950 mm. El segundo tipo climático, presente solo en la porción noroeste de la comunidad, es el templado subhúmedo con lluvias en verano C(w)O(W), cuya temperatura media anual varía entre 17- 19 °C; y presenta una precipitación pluvial anual de 650 a 700 mm (INEGI, 2000a; INEGI, 2000b).

El verdadero contraste existe en la fauna. En el 2005, Tovar-Liceaga hizo una comparación entre la fauna fósil colectada de Santa Cruz Nuevo con la Reciente. Encontró que de toda la fauna fósil colectada (mastofauna y herpetofauna), el 18% de las familias correspondían a megafauna que está extinta para Norteamérica, el 32% cambió su distribución geográfica y el 50% continúa en la localidad. ¿Por qué la biota cambió si las condiciones ambientales son similares? La respuesta se puede encontrar en los otros 30,000 años no registrados.

La localidad Axamilpa se encuentra a 50 kilómetros de distancia de Santa Cruz Nuevo siendo un depósito más joven, depositado probablemente entre los límites de la MIS 3-MIS 2.

Contrario a Santa Cruz Nuevo, en Axamilpa la tasa de sedimentación es baja, con presencia de varios suelos poco desarrollados pero con un mayor contenido de arcilla (superior al 60% en la mayoría de los suelos) y cantidades de arenas inferiores al 10%. Existen varios horizontes A poco profundos.

De las cuatro unidades pedostratigráficas, el análisis micromorfológico muestra suelos más desarrollados en las unidades gleyca y húmica mientras que la vértica y cálcica tienen un mayor componente sedimentario. En los paleosuelos más desarrollados hay evidencia de actividad biológica.

En el caso del contenido fósil también se observan diferencias muy contrastantes. La fauna fósil de Axamilpa (*Testudinidae*, *Mammuthus columbi*, *Cuvieroniu* *tropicus*, *Equus* *sp.*, *Bison* *sp.*, *Paleolama* *sp.*, *Glyptotherium* cf. *G. cylindricum*, y *Glossotherium* (*Paramylodon* *harlani*) es menos diversa y corresponde principalmente a restos de megafauna. La ausencia de microvertebrados puede estar ligada a tasas de sedimentación baja que permite la exposición de los huesos a los factores del intemperismo.

El registro de isótopos estables de carbono ($\delta^{13}\text{C}$) de las diversas unidades pedológicas de Axamilpa indica climas más húmedos que en Santa Cruz Nuevo (Cuadro 5). El registro de fitolitos junto con los pocos restos de megafauna que pudieron ser correlacionados a los paleosuelos permitió hacer una interpretación más completa de los paisajes que dominaron el final de la MIS 3 hasta mediados de la MIS 2.

Cuadro 5. Porcentajes de las formas de fitolitos presentes en las diversas unidades pedoestratigráficas de la secuencia Axamilpa.

	Estagnogleyca	Vértica	Cálcica	Húmica
Pastos C3	29.1%	19.4%	45.0%	48.0%
Pastos C4	3.4%	32.4%	20.5%	19.8%
Coníferas	44.4%	7.2%	16.0%	5.0%
Otras formas C3	15.4%	7.7%	4.0%	8.4%
Derivados animales		30.2%	8.5%	16.3%
Formas no-diagnósticas	7.7%	3.2%	6.0%	2.5%

El registro de fitolitos de la unidad estagnogleyca indica una alta abundancia de coníferas, lo cual nos hace suponer que debieron dominar los bosques ya que las coníferas no son grandes productoras de fitolitos (Dinan y Rowlett, 1993). Los bosques de coníferas regularmente se encuentran asociados a climas templados-fríos sin embargo, también se les localiza en climas semiáridos, semihúmedos y francamente húmedos (Rzedowski, 1978). En el área de estudio, la asociación de fitolitos (Cuadro 5) sugiere condiciones de humedad por dominancia de plantas con metabolismo C3. Es probable que esta unidad sea correlacionable con la del perfil San Lucas, San Juan Raya, también dentro de la Reserva de la Biósfera Tehuacán-Cuicatlán. En el perfil San Lucas, Canul-Montañez (2008) indica la presencia de un bosque de pino a los $25,220 \pm 160$ ^{14}C años que se caracteriza por establecerse a temperaturas entre los 10 – 20°C con precipitación media anual de entre 600-1000 mm (Rzedowski, 1978).

Durante la formación de la unidad vértica las condiciones se volvieron más secas con una alta dominancia de pastos C4 y una disminución significativa de los fitolitos de coníferas. En el diagrama polínico de Canul-Montañez (2008) se observa una tendencia similar. Ella reporta una disminución significativa de granos de polen de *Pinus* y un aumento de *Quercus* y *Alnus* de alrededor del 5% así como un mayor porcentaje de pastos de la familia Asteraceae (19%) y nopales (género *Opuntia*).

Durante la formación de las siguientes dos unidades (cálcica y húmica) se observa un aumento en pastos C3 (Cuadro 5) y sólo en la Cálcica se observa una mayor proporción de coníferas (16%).

Se han podido correlacionar los fósiles de *Cuvieronius tropicus* y *Glossotherium* (*Paramylodon*) *harlani* con la unidad cálcica mientras que *Equus* sp. y *Mammuthus* sp. con la húmica. El análisis de isótopos de $\delta^{13}\text{C}$ (Cuadro 6) del esmalte de *Cuvieronius tropicus* y

Equus sp. muestra una preferencia en la dieta hacia vegetación mixta lo cual es consistente con el tipo de fitolitos encontrados.

Cuadro 6. Valores de isótopos de carbono obtenidos de dientes de mamíferos fósiles de Axamilpa.

Género	Unidad	$\delta^{13}\text{C}_{\text{VPDB}}$	$\delta^{18}\text{O}_{\text{VPDB}}$	Con factor de enriquecimiento 14.1 ‰
<i>Cuvieronius tropicus</i>	Unidad Húmica	-2.93	-6.10	-17.03
<i>Equus</i> sp.	Unidad Cálcaica	-2.73	-0.90	-16.83

Con base en los resultados de Axamilpa, se sugiere que al final de la MIS 3, los ecosistemas forestales debieron dominar la parte sur del estado de Puebla. Hacia la transición entre la MIS 3 - MIS 2 hubo una reducción del ecosistema forestal y un aumento de gramíneas con variaciones en la humedad durante la MIS 2.

Contrario a Santa Cruz Nuevo, los ecosistemas aquí reconstruidos difieren mucho del Presente. En el Presente los ecosistemas dominantes corresponden a matorral crasicaule, chaparrales, palmares, pocas áreas con bosque de encino y pastizales con mezquite (Arredondo-Gutiérrez, 2009). El clima es tipo B, clima seco, donde la precipitación es menor a los 500 mm por año (Rzedowski, 1978).

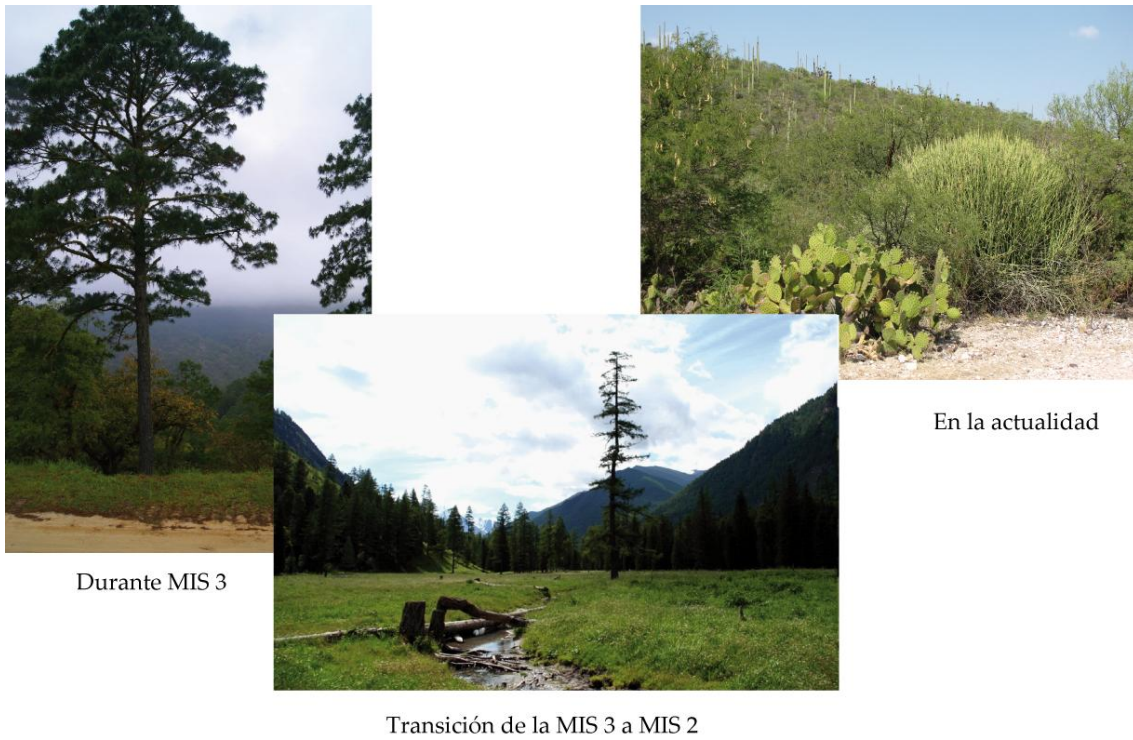


Figura 7. Modelo de evolución del paisaje de Axamilpa durante el Pleistoceno tardío.

Asumiendo que las dos localidades responden a los cambios ambientales presentes durante la MIS 3 - MIS 2, se observa una alternancia entre condiciones húmedas y secas que explicarían el porqué de los cambios observados en la fauna.

Oscilaciones climáticas en el sur de México

Se han reconocido 25 ciclos Daansgaard-Oeschgard y 6 ciclos Heinrich, de los cuales 16 (17-3) están conferidos a la MIS 3 y sólo uno (2) a la MIS 2 (Wolff *et al.*, 2010). Con pocas excepciones (Lago de Chalco, Zacapú y Petén - Itza), las cuencas presentes en el centro-sur de México registran solamente el final de la MIS 3 y MIS 2 y no han sido correlacionadas con las oscilaciones climáticas a escala milenaria.

Considerando que hacia la sierra sur de México existen pocos lagos que acarrearán agua durante el Pleistoceno tardío (Mueller *et al.*, 2012) y que, bajo pocas excepciones, la mayoría de las cuencas lacustres son comunes a partir de los 25,000 ¹⁴C años (Caballero *et al.*, 2010), tener otros proxies que registren los cambios ambientales ayuda en la reconstrucción climática.

Asumiendo que los cambios ambientales globales quedan registrados en los sedimentos, suelos, asociaciones bióticas, etc., ¿podrían las secuencias pedoestratigráficas ser utilizadas para discernir las oscilaciones climáticas experimentadas en el sur de Puebla a escala milenaria?

A nivel global se han hecho estas correlaciones haciendo uso de las secuencias de loess-paleosuelos (por ejemplo, Kadereit *et al.*, 2013; Haesaerts *et al.*, 2009; Rutter *et al.*, 1998; Terhost *et al.*, 2014; Wang *et al.*, 2003). Pero en el caso de México que no cuenta con registros de loess, se plantea la pregunta ¿las secuencias pedoestratigráficas podrían dar indicios de estas oscilaciones en el clima?

En términos generales, muchos procesos actúan juntos para formar cualquier perfil de suelo, es difícil discutir la formación del suelo como un función de un proceso en específico (Birkeland, 1999). Sin embargo, el clima es el factor versátil que afecta virtualmente a todos los fenómenos pedológicos (Gennadiyev y Chernyanskii, 2006). El

clima de los suelos es un tipo especial de microclima, el cual hace referencia a las condiciones de humedad, temperatura y otros índices climáticos dentro de los poros del suelo (Retallack, 2001). La precipitación anual y su distribución en estaciones junto con la evapotranspiración dictaminan el grado de humedad del suelo, la profundidad a la que el agua se percola, las reservas de agua obtenidas por las plantas y el suplemento de agua absorbido por la microbiota del suelo. La dependencia del suelo al clima se manifiesta por la zonalidad climática de la cobertura del suelo, por ejemplo, la distribución del suelo sobre la superficie terrestre asociada a los cinturones térmicos y regiones con diferentes niveles de humedad (Gennadiyev y Chernyanskii, 2006). En pocas palabras, el clima juega un papel importante en la formación y diferenciación del suelo siempre y cuando esté bien drenado. En los suelos bien drenados, el clima del suelo es muy similar al clima regional, sin embargo, en aquellos suelos inundados no existe una relación. La temperatura y oxigenación de los suelos saturados en agua dependen de las tasas locales del flujo del agua subterránea más que de las condiciones atmosféricas (Retallack, 2001).

A pesar de que los suelos desarrollados sobre las planicies de inundación suelen estar saturados en agua por su cercanía al canal ¿podrían, de alguna forma, dar indicios de los cambios ambientales?

Se sabe que el estudio de los sistemas fluviales es muy útil en las reconstrucciones ambientales, ya que en varias localidades la tectónica no ha jugado un papel predominante por lo que se asume que los cambios ambientales han sido registrados. Aunado a los cambios en las descargas de los ríos, la presencia de los paleosuelos da una visión más clara de las condiciones que reinaron alrededor de la cuenca, como lo ha demostrado el estudio de Borejsza y Frederick (2010).

En México, en varias secuencias pedológicas aluviales se observan grandes paquetes de sedimentos intercalados con paleosuelos a los cuales como ya ha señalado Solleiro-Rebolledo *et al.* (2003) no se le ha prestado suficiente atención pese a que varios fósiles se han recuperado de ellos.

La mayoría de los estudios para relacionar la geomorfología aluvial y clima datan del Holoceno o la transición entre el Pleistoceno-Holoceno. Lo que buscan estos estudios es observar los cambios ambientales y la influencia que generaron los establecimientos humanos sobre los paisajes (Por ejemplo, Butzer *et al.*, 2008; Curtis *et al.* 1998; McClung de Tapia *et al.*, 2005; Piperno *et al.*, 2007).

En el caso del Pleistoceno se reconocen las secuencias aluviales de Nochixtlán (Mueller *et al.*, 2012), Teotihuacán (Solleiro-Rebolledo *et al.*, 2003), Huexoyucan (Solís *et al.*, 2012; Tovar *et al.*, 2013), Axamilpa (Tovar *et al.*, 2014b) y Santa Cruz Nuevo (Tovar *et al.*, 2014a).

Santa Cruz Nuevo representa la parte final de la MIS 3. En esta localidad se observan grandes paquetes sedimentarios intercalados con suelos poco desarrollados. En el área de estudio no existe evidencia de movimientos tectónicos durante el Pleistoceno por lo que se asume que la alta tasa de sedimentación debió darse como respuesta a los cambios en el ambiente.

Asumiendo que la secuencia de Santa Cruz Nuevo respondió a los cambios ambientales, se sugiere que durante los periodos secos la vegetación era escasa, permitiendo una mayor erosión de los sedimentos. La tasa de sedimentación aumentó depositando grandes paquetes sedimentarios. Durante los periodos húmedos, el incremento en vegetación frenó o disminuyó la erosión, favoreciendo la formación de

suelo. La duración de los periodos húmedos debió ser corta debido a que los suelos son incipientes.

En otras localidades con paleosuelos no-aluviales donde las tasas de sedimentación no son significativas, se observan suelos poligenéticos. Los suelos poligenéticos son suelos que registran múltiples firmas morfológicas, mineralógicas y químicas debido a cambios en los patrones geográficos de los climas y se mantienen hasta que se vuelven a establecer nuevos límites (Nikiforoff, 1953). De forma más concreta, los suelos poligenéticos son aquellos que se forman en más de un régimen climático.

Estos suelos poligenéticos se han asociado con cambios abruptos en la precipitación y/o temperatura lo que genera nuevas propiedades en el suelo sin que se pierdan las preexistentes. Los suelos poligenéticos de la Faja Volcánica Transmexicana son más comunes a finales de la MIS 3 (Sergey Sedov, comunicación personal).

Los suelos PT2 (29,000-24,000 ¹⁴C años) y PT3 (42,000-29,000 ¹⁴C años) presentes en el Nevado de Toluca a pesar de tener características de pedogénesis húmeda también presenta evidencias de fluctuaciones húmedas/secas (Sedov *et al.*, 2003).

El suelo SP2 del perfil San Pablo (24070 ± 350 ¹⁴C años) presenta características gleycas sin embargo combina signos de pedogénesis húmeda y seca (Solleiro-Rebolledo *et al.*, 2011). En Tepexpan de los 27,000-20,000 años predominaron los bosques de pino pero alrededor de los 20,000 años se observa un cambio de vegetación con una disminución en las especies forestales y un aumento en las herbáceas indicando un cambio hacia condiciones más secas (Sedov *et al.*, 2010). En Axamilpa ocurre algo similar, en la unidad gleyca, que data de finales de la MIS 3, está establecido un bosque de coníferas. A partir de la unidad vértica, el bosque decrece sustancialmente y hay un aumento en las gramíneas.

En el caso del perfil San Pablo, en Teotihuacán, se observa que para finales de la MIS 3, los suelos (SP4 y SP3) presentan signos de pedogénesis húmeda como la iluviación de arcilla y procesos redoximórficos. Solleiro-Rebolledo *et al.* (2011) lo asocian con un ecosistema forestal sin dejar de mencionar que existen características indicativas de climas secos (procesos vérticos, precipitación de carbonatos, zooturbación) intercaladas en el mismo suelo. Los autores correlacionan el suelo SP4 con el suelo TX2 de la secuencia de Tlaxcala que tiene una edad entre los 38,000-29,000 años AP y que también presenta procesos vérticos (Sedov *et al.*, 2009).

En el caso de las dos secuencias estudiadas, Santa Cruz Nuevo y Axamilpa, los eventos secos fueron intercalados con eventos húmedos (Tovar *et al.*, 2013 y Tovar *et al.*, 2014a y b) que se desconoce su edad aunque se infiere que debieron ser más antiguo que 30,000 ¹⁴C años para Santa Cruz Nuevo y probablemente deben estar alrededor de los 29,000-25,000 ¹⁴C años para Axamilpa.

A partir de los 25,000 ¹⁴C años los suelos siguen mostrando oscilaciones climáticas pero se desconoce el momento en el que ocurrieron.

Además de los cambios en las tasas de sedimentación que dan indicios de la respuesta geomorfológica a los cambios ambientales, los suelos por si mismos ofrecen evidencia de las condiciones en las que se formaron. De hecho Mueller *et al.* (2012), estudiando la secuencia de Nochixtlán, mencionan que los suelos cumúlicos con edades superiores a los 10,000 años no tienen análogos actuales obvios en las sierras mexicanas.

Durante la MIS 3 las asociaciones no análogas o disarmónicas son más comunes. Lo cual es de esperar si se considera que la relación entre el ambiente y los organismos es bidireccional ya que tanto los organismos modifican al ambiente como los cambios ambientales inciden en la selección natural y evolución (Phillips, 2009).

Correa-Metrio *et al.* (2012b) sugirió que las asociaciones no-análogas se formaron durante los ciclos Heinrich, particularmente H6-H3, como respuesta a los cambios abruptos en las condiciones ambientales. Durante estos cambios las especies migraron hasta encontrar su equilibrio bioclimático sin embargo, estas migraciones fueron de corta distancia.

Correa-Metrio *et al.* (2012b) también señaló que los cambios en temperatura durante los eventos Heinrich no fueron tan drásticos (-2.5 y 2°C cada 100 años) por lo que el contraste entre las altas tasas de cambio ecológico pero bajas tasas de cambio climático durante H6-H3 sugiere que las asociaciones no análogas fueron el resultado de climas no análogos.

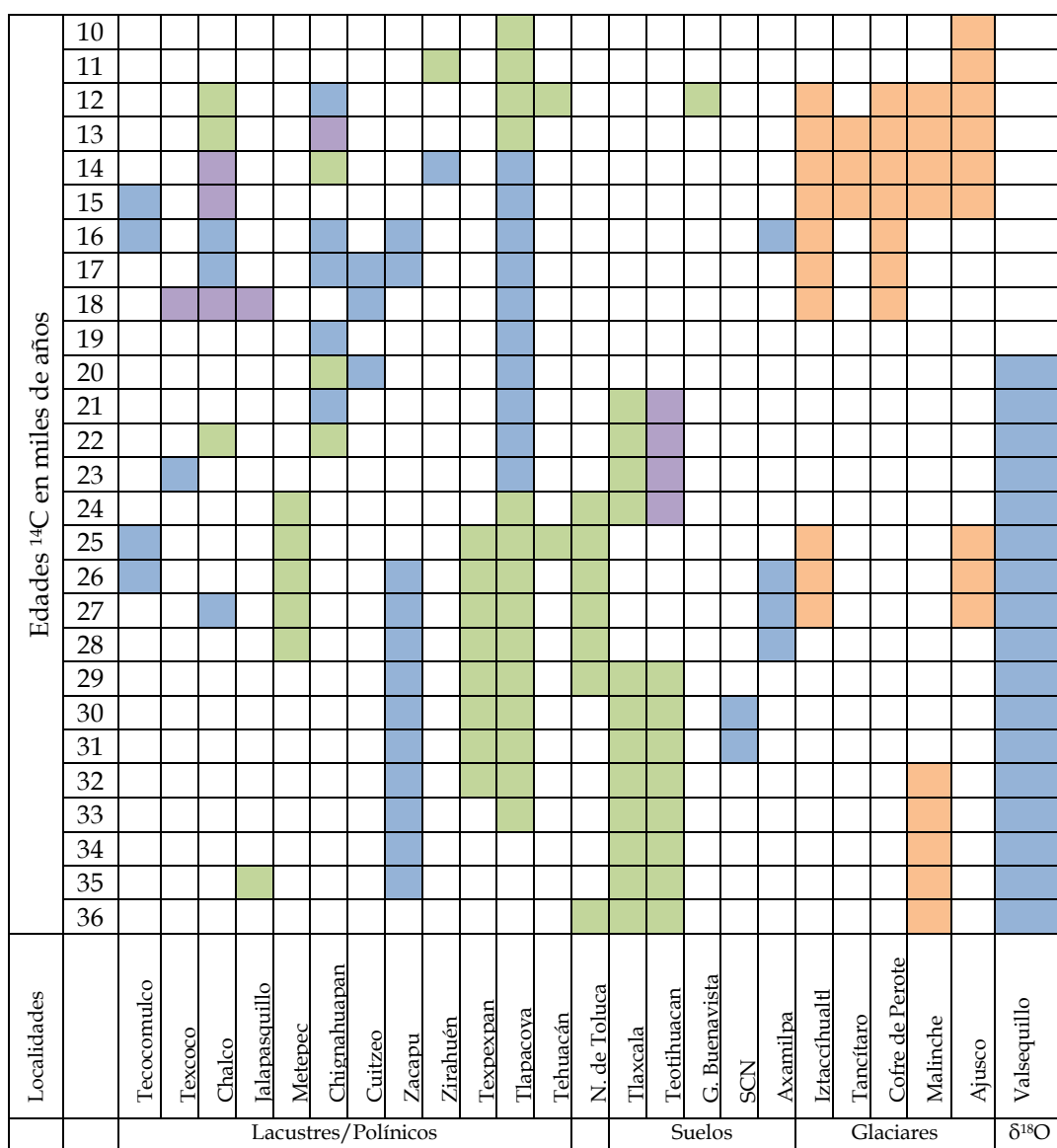
La Figura 8 resume a grandes rasgos las principales firmas climáticas presentadas en varios trabajos del centro-sur de México. Las edades utilizadas se dan en años de radiocarbono A.P. para fines comparativos por lo que aquellos estudios que no presentan dataciones de radiocarbono fueron descartados.

En la Figura 8 se observan varios huecos en la respuesta climática para una misma localidad y no se observa una similitud en las condiciones climáticas entre distintas localidades. Esto puede deberse, entre varios factores, al grado de generalidad de la tabla, y a que las edades de radiocarbono regularmente están restringidas a ciertos horizontes o capas, por lo que se conocen las tendencias climáticas pero no el tiempo exacto en el que ocurrieron.

Generalmente los autores tienden a interpretar las señales ambientales abarcando grandes periodos de tiempo, regularmente varios miles de años (Cuadro 7), y a veces hacen algunas acotaciones sobre pequeños reversos o señales que les indican un cambio

rápido y drástico en las condiciones ambientales (por ejemplo, Sedov *et al.*, 2009; Solleiro-Rebolledo *et al.*, 2011).

Figura 8. Representación gráfica de los datos obtenidos de distintos estudios lacustres/polínicos, paleosuelos, isótopos y glaciales. ■ Registros secos, ■ Registros húmedos, ■ Registros que muestran tendencia hacia condiciones secas (mixto), ■ Registros glaciales



Cuadro 7. Comparación entre algunas localidades del centro-sur de México y su respuesta a los cambios ambientales ocurridos al final del Pleistoceno.

Localidad	Fin de MIS 3 (57-29 ka) Alrededor de los 30 ka	MIS 2 (29-14 ka)	Material estudiado	Referencias
La Malinche	Avance glacial (36-32 ka) Condiciones frías y húmedas	(>15-12 ka) Condiciones frías y húmedas	Morrenas	Heine, 1988
Ajusco	Avance glacial Santo Tomás (>25 ka) Marqués (>27 ka) Condiciones frías y húmedas	(<16->10 ka) Condiciones frías y húmedas	Morrenas	White y Valastro, 1984; White, 1987
Hueyatlaco		Avance glacial Hueyatlaco-2 (14-12 ka) Hueyatlaco-1 (c. 16-14,8 ka) Condiciones frías y húmedas	Morrenas	(Vázquez-Selem, 2000)
Barranca Caulapan en Valsequillo, Puebla	Condiciones más secas que en el Presente	Frías y húmedas	$\delta^{18}\text{O}$ y $\delta^{13}\text{C}$ de caracoles terrestres	Stevens <i>et al</i> , 2012
Tecocomulco, Estado de México	Ausencia de diatomeas con presencia de una capa rica en carbonatos		Diatomeas	Roy <i>et al.</i> , 2009
Texcoco, Estado de México		Incremento en la salinidad alrededor de los 23 ka		Bradbury, 1971, 1989; Ramírez-Nava, 2002
Texcoco, Estado de México	climas templados subhúmedos con periodos secos durante 35- 20 ka		Polen	Lozano-García y Xelhuantzi-López, 1997
Lago de Chalco, Estado de México	lago somero y alcalino	Condiciones de agua dulce alrededor de los 22 ka	Diatomeas	Caballero-Miranda, 1997.
Nevado de Toluca, Estado de México		Climas húmedos y fríos (forestales) 28-11,600	Paleosuelos	Sedov <i>et al</i> (2001)

Este grado de generalidad, dado ya sea por la interpretación del autor o la restricción del recurso, impide hacer una comparación directa con las oscilaciones climáticas milenarias.

El depósito de Santa Cruz Nuevo debió formarse entre los GI 7-5. Está caracterizado por intercalaciones entre grandes paquetes sedimentarios que aquí se asume se formaron en periodos secos y paleosuelos incipientes que se formaron en periodos relativamente húmedos. Asociado a los paleosuelos se han reportado faunas disarmónicas (Tovar y Montellano, 2005). Las asociaciones disarmónicas pueden ser resultado de procesos tafonómicos (por ejemplo, Semken Jr. *et al.*, 2010) o como ha sugerido Correa-Metrio *et al.* (2012b) para el Lago Petén Itzá, Yucatán debido a cambios climáticos drásticos.

Es probable que en el caso de Santa Cruz Nuevo, la asociación faunística disarmónica sea de origen tafonómico. Sin embargo, indicaría que muy cerca de la zona de estudio hubo varios ecosistemas, contrario al Presente.

La presencia de varios ecosistemas cercanos o asociaciones no-análogas fueron consecuencia de cambios climáticos abruptos y probablemente sean la causa del cambio biótico observado en ambas localidades.

Conclusiones

El uso de varios proxies da una imagen más completa de los paisajes que estuvieron presentes en el sur de Puebla al final de la MIS 3 y MIS 2 permitiendo correlacionar el registro biótico con los paleosuelos.

Los isótopos de carbono obtenidos del suelo y el registro de fitolitos en la secuencia de Axamilpa permitieron especificar los tipos de ecosistemas presentes a lo largo del tiempo, lo cual fue muy útil para poder correlacionarla con otros registros como el de Tehuacán, que está basado en polen. Así mismo la presencia de *Cuvieronius tropicus* y *Equus* sp. junto con los isótopos estables de carbono obtenidos de sus dientes ayudó a conocer sus preferencias en dieta, lo cual ayudó a dar más características acerca de la vegetación.

En el caso de Santa Cruz Nuevo, la alta paleodiversidad permitió reconocer los ecosistemas cercanos y con base en los isótopos de carbono reconocer que las plantas más abundantes debieron tener metabolismo CAM y corresponden principalmente a suculentas.

Se observó que, a pesar de la limitante en la escala cronológica, los paleosuelos registran hasta las pequeñas variaciones que debieron existir en el ambiente. En el caso de Santa Cruz Nuevo, la intermitencia entre las altas de sedimentación y la formación de paleosuelos incipientes indica la dinámica que debió prevalecer a finales de la MIS 3. En otros registros paleopedológicos esta dinámica se manifiesta a través de los suelos poligenéticos. Estas variaciones climáticas, que se observan principalmente al final de la MIS 3, probablemente están asociadas con los cambios milenarios que se registran en algunas secuencias polínicas del centro y sur de México.

No se pudo establecer una correlación entre las oscilaciones climáticas registradas en las secuencias estudiadas con otras cuencas nacionales y/o globales debido tanto al tipo de registro como a la escala temporal. Una mejora en la técnica de datación podría llegar a resolver el problema temporal. Sin embargo, siempre se tendrá que usar a los paleosuelos junto con otros proxies debido a que los suelos se forman en un gran intervalo de tiempo y a menos que sean sepultados, manifestarán las distintas firmas ambientales que estuvieron presentes durante su formación.

El objetivo de este trabajo no fue determinar una causante para la extinción de la megafauna ni las causas de extirpación de las especies presentes en ambas localidades, sin embargo, es muy probable que la causante para ambos fenómenos esté ligada a los cambios climáticos experimentados durante el final del Pleistoceno-inicios del Holoceno.

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