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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 habitats da megafauna do Pleistocénico tardio

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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 micromofología 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 tardio, 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 micromofología 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 escuros 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, δ^{13}C, Puebla, Tlaxcala, MIS3, MIS2

PALABRAS CLAVE
Paleoambientes, δ^{13}C, Puebla, Tlaxcala, MIS3, MIS2

PALAVRAS-CHAVE
Paleoambientes, δ^{13}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 south-west 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 dentralis,* 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).

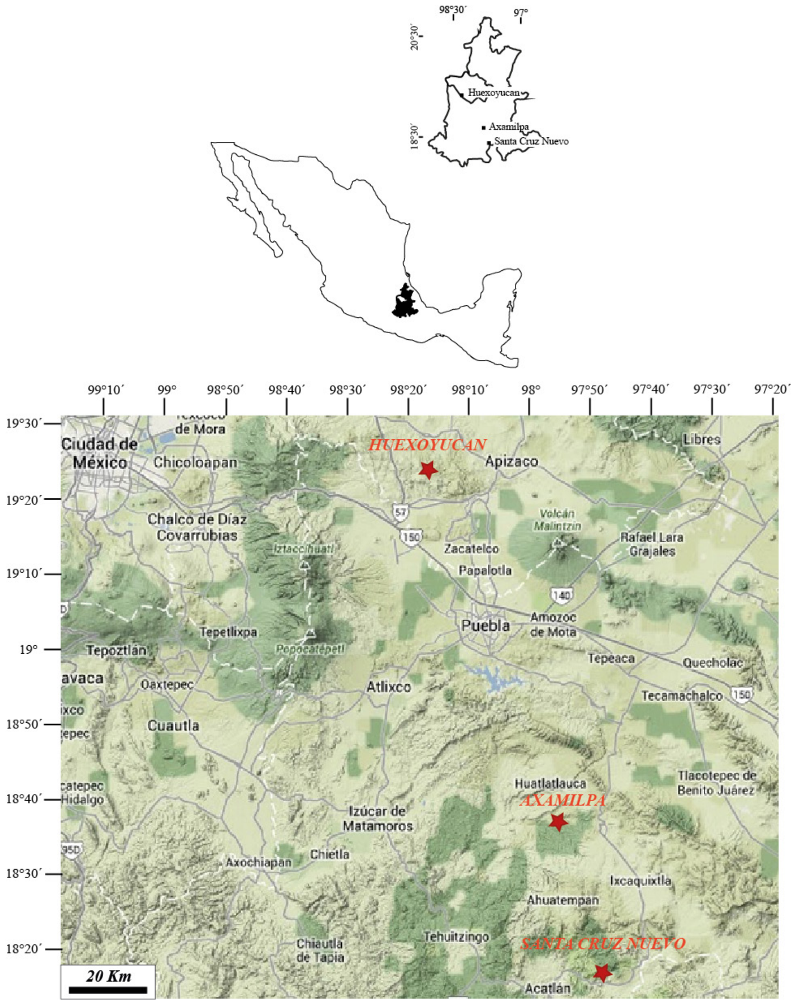

Figure 1. Location of the study areas: Huexoyucan, in the state of Tlaxcala, and Axamilpa and Santa Cruz Nuevo, in the state of Puebla. The state limits are marked with discontinuous white lines.

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 tephras 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.), bisons (*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 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 δ^{13}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).

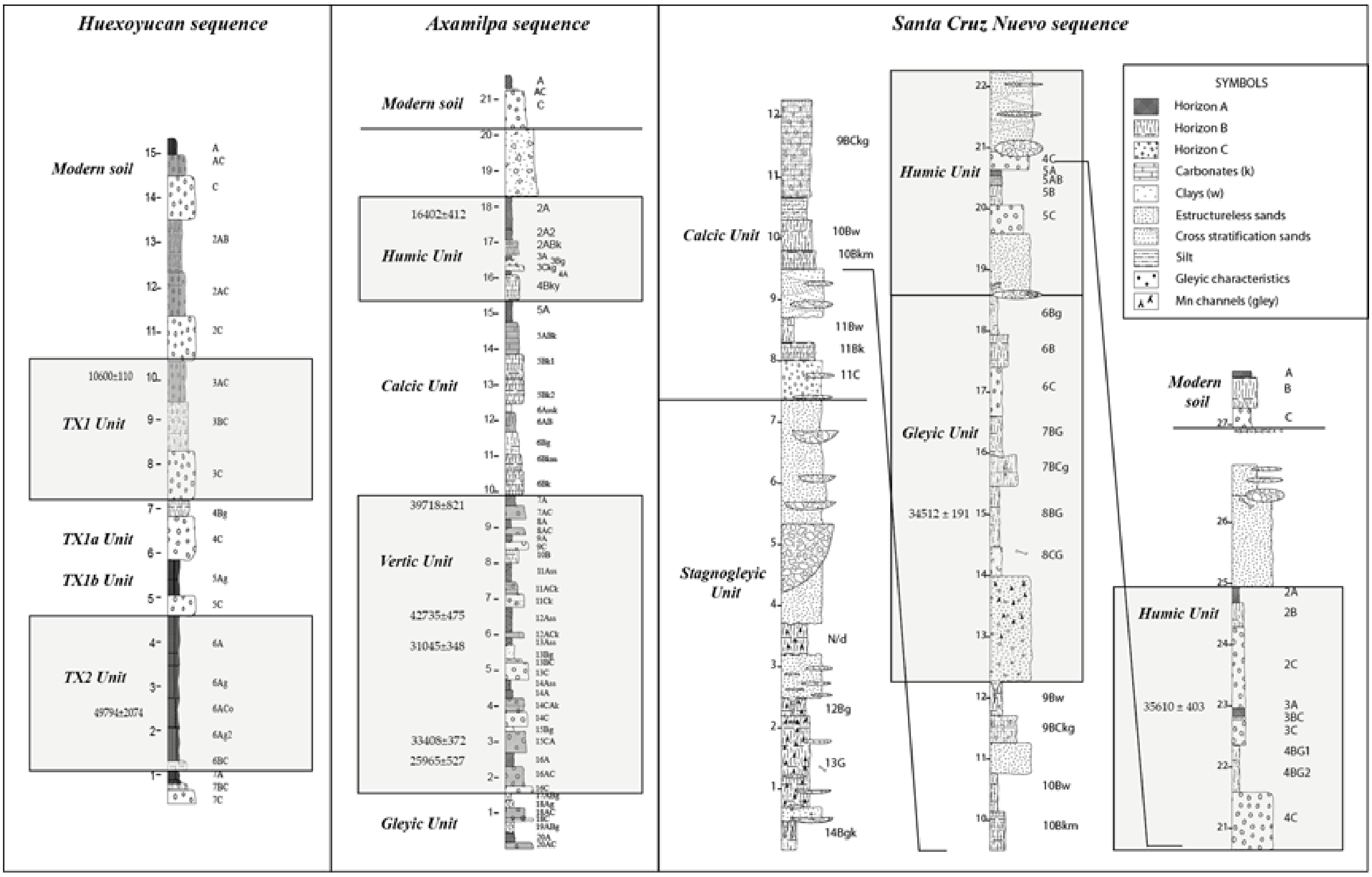

Figure 2. Stratigraphic schemes of the Huexoyucan, Axamilpa and Santa Cruz Nuevo paleosol sedimentary sequences. The gray square indicates de pedological units analyzed in this study.

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.

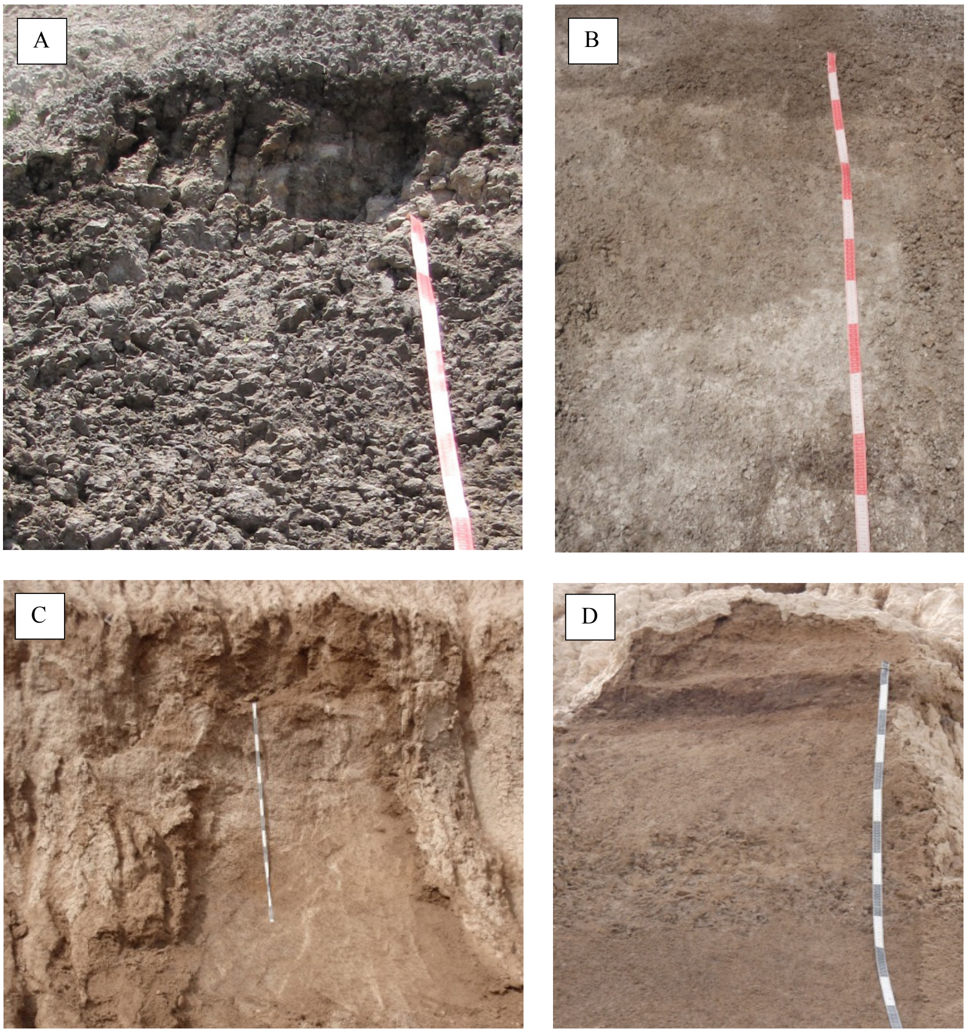

Figure 3. The views of the four pedostratigraphic units analyzed in this study. **A.** The Vertic Unit of Axamilpa. **B.** The Humic Unit of Axamilpa. **C.** The Gleyic Unit of Santa Cruz Nuevo. **D.** The Humic Unit of Santa Cruz Nuevo.

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 δ^{13}C.

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

	Radiocarbon ages AP	Calibrated ages AP[1]	δ^{13}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		
Humic Unit			
3A	31 680 ± 120 (Beta-277570)	35 610 ± 403	-19.5
Gleyic Unit			
8Bg	30 380 ± 220 (Beta-277569)	34 512 ± 191	-22.5
	Axamilpa		
Vertic Unit			
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
Humic Unit			
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).

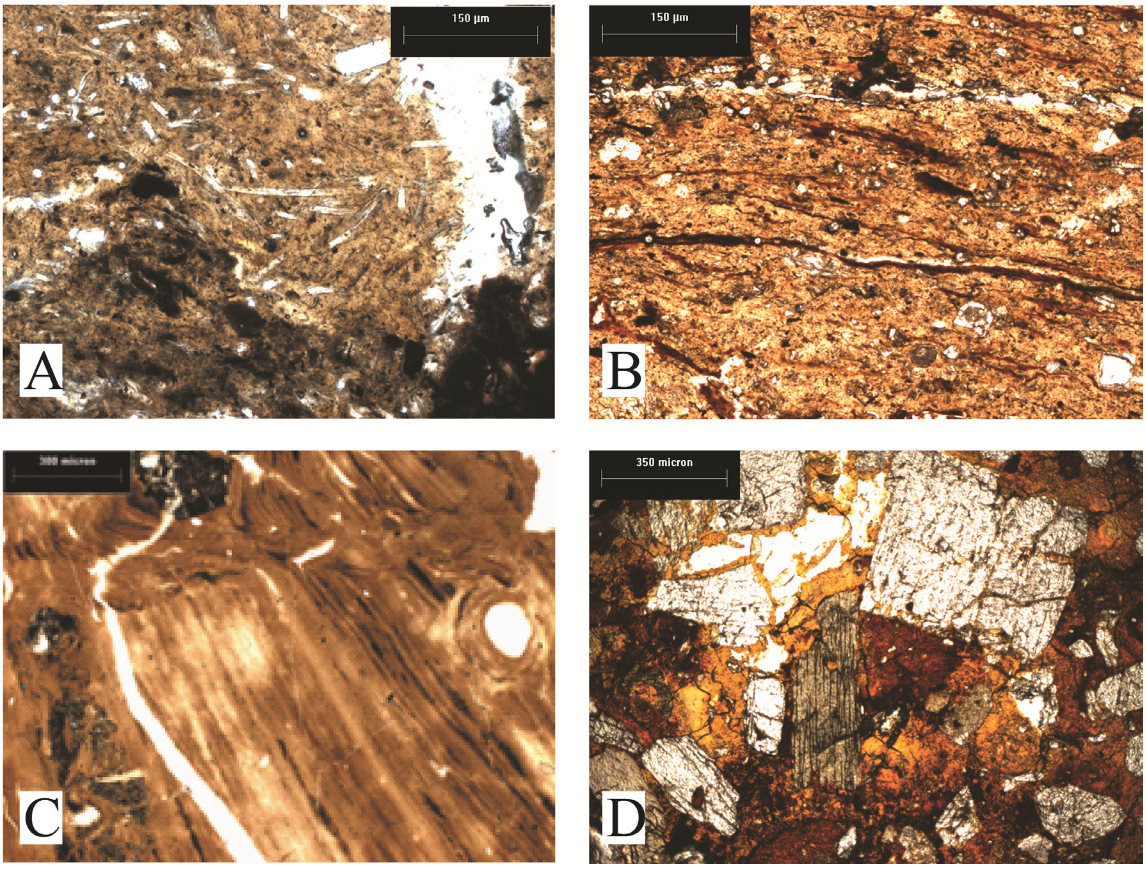

Figure 4. The micromorphology of the TX2 humus horizon, Huexoyucan section. **A.** Silica microfossils in the groundmass, PPL. **B.** Sedimentary microlamination, PPL. **C.** Microlaminated clay infilling, PPL. **D.** Weathered rock fragment, yellow clay fills the spaces between primary mineral grains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

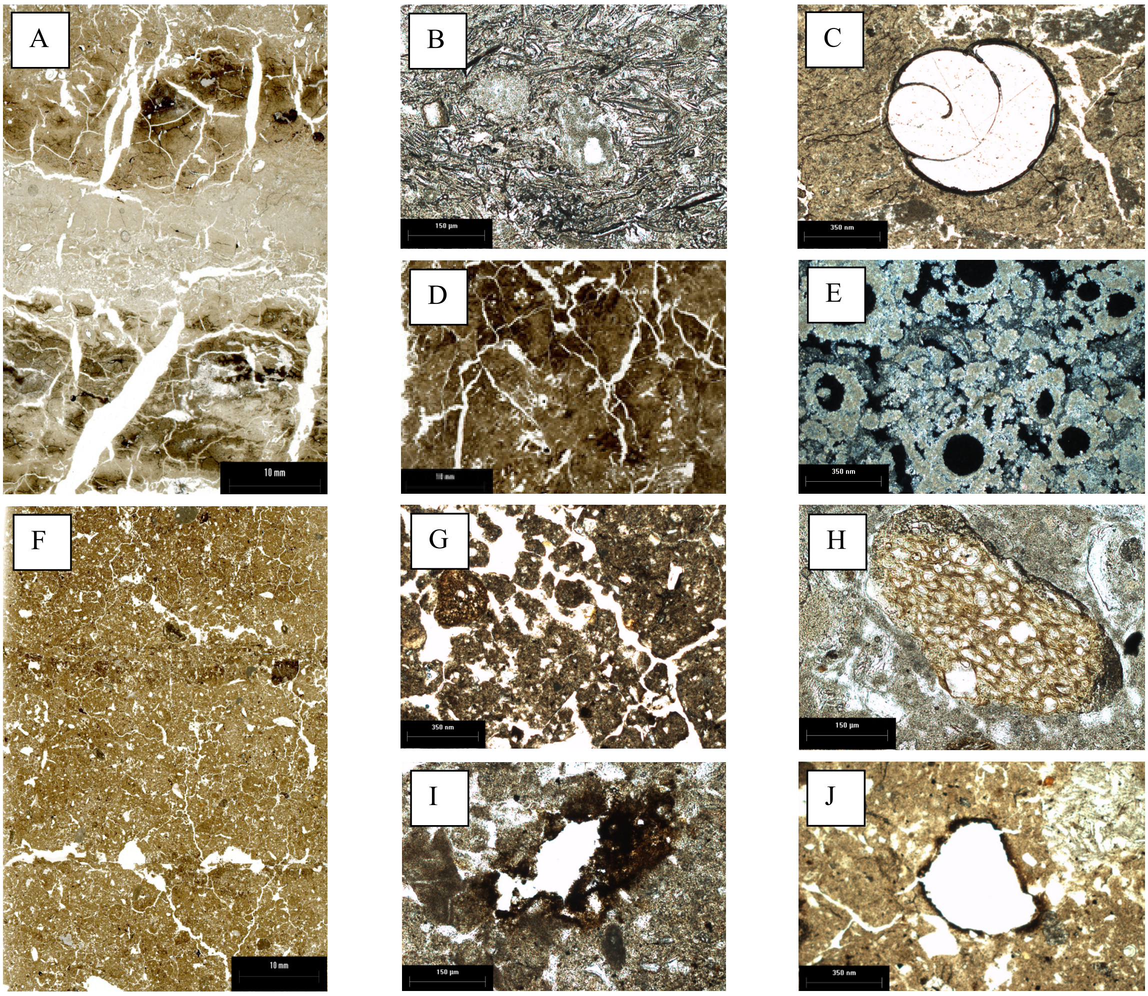

Figure 5. The micromorphology of Axamilpa. A-E correspond to the Vertic Unit. **A.** Scanned thin section of the 12ACk paleosol of the Vertic Unit showing sedimentary lamination and fracturing. **B.** Diatoms, PPL. **C.** Gastropod valve. PPL. **D.** Thin section of the paleosol 13Ass of the Vertic Unit with their fractures caused by contraction. PPL. **E.** Microsparitic hypocoatings of the same 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.

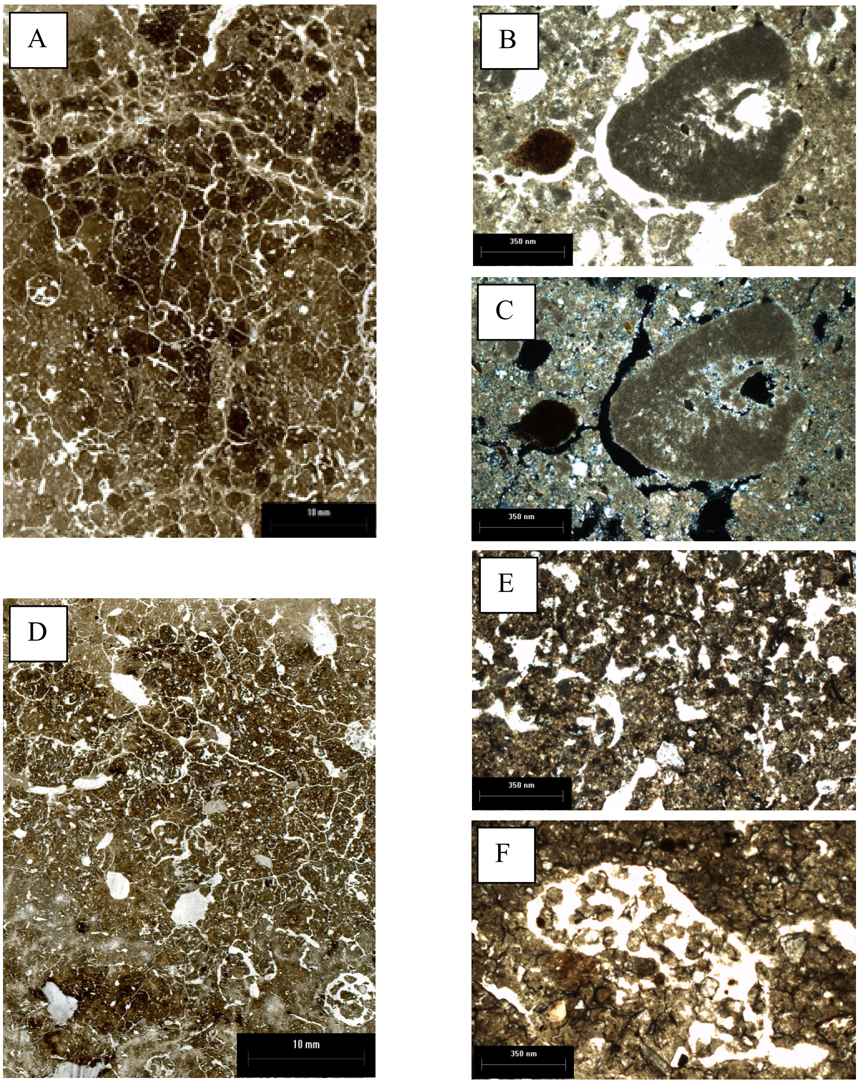

Figure 6. The micromorphology of Santa Cruz Nuevo. A-C correspond to Gleyic Unit. **A.** Scanned thin section of the 6Bg paleosol of the Gleyic Unit: compact arrangement, pores – predominantly thin fissures. **B.** Small ferruginous (left) and large micritic (right) nodules, PPL. **C.** Same as B, note 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*, *Hantszchia*, *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 of 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 δ^{13}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-Amaranthacea), grasses (Poaceae), and Cyperaceae (Solís-Castillo et al. 2012).

In the Vertic Unit, the values of δ^{13}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 δ^{13}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 δ^{13}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 templates climates, feeding on leaves along the water bodies (Gillete 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 pedostratigraphic 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 $\delta^{13}C$ 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 $\delta^{13}C$ 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 $\delta^{13}C$ 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 $\delta^{13}C$ 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 δ^{13}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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