Quaternary International 287 (2013) 73–82

Contents lists available at SciVerse ScienceDirect

Quaternary International

journal homepage: www.elsevier.com/locate/quaint

Paleoenvironment of the Toropí Formation (Upper Pleistocene), Corrientes province (Mesopotamian region, Argentina): A phytolith approach

Georgina Erra [a,*], Margarita Osterrieth [b], Alfredo E. Zurita [a], Analía Francia [a], Alfredo A. Carlini [c]

[a] Centro de Ecología Aplicada del Litoral (CECOAL-CONICET), Corrientes, Argentina
[b] Centro de Geología de Costas y del Cuaternario, Facultad de Ciencias Exactas y Naturales, UNMdP, Argentina
[c] División Paleontología de Vertebrados, Museo de La Plata and CONICET, Argentina

ARTICLE INFO

Article history:
Available online 7 September 2012

ABSTRACT

Two Pleistocene sedimentary units are recognized in the Corrientes province, Argentina: the Toropí and Yupoí formations. These sediments have proven productive for fossil vertebrates, but few macrofossils have been recovered. To remedy this situation, plant silica (phytoliths) were extracted from the sediments, enabling a direct comparison of paleovegetation data and information based on previous study of vertebrates. The studied samples ($n = 28$) come from two profiles from the Toropí Stream (28°36′S; 59°02′W), near Bella Vista, Corrientes, from which two Quaternary mammals, *Lestodon* (Xenarthra) and *Hippocamelus* (Artiodactyla), have previously been excavated. All samples were productive and contained both non-plant biogenic silica (diatoms, sponge spicular, chrysophyte cysts) and phytoliths. Phytolith assemblages were dominated by morphotypes diagnostic of grasses, in particular C_3 pooids, C_4 chloridoids, and C_3 or C_4 panicoids (or related grasses in the PACMAD clade). Rare phytoliths of palms and other woody or herbaceous dicotyledonous angiosperms were also present. This combination of C_3 and C_4 grasses, and rare palms and other forest indicators, indicates grass-dominated habitats with groves with palms and other trees/shrubs along rivers, growing under a relatively warm and dry climate. This mixed plant community reflects shifting biogeographic affinity with the Chaco-Pampean plain and inter-tropical regions, respectively, linked to the frequent climatic-environmental fluctuations during the Late Pleistocene.

© 2012 Elsevier Ltd and INQUA. All rights reserved.

1. Introduction

During most of the Cenozoic, South America was an island continent, lacking any terrestrial connections to other continental land masses. This long-lasting geographical isolation resulted in a highly endemic vertebrate fauna and flora that cannot be easily compared to other continents (Simpson, 1980; Ricklefs, 2002; Morley, 2003) This biota, in particular the fauna, was significantly restructured during the Great American Biotic Interchange (GABI), which peaked around 3 Ma with the establishment of a land bridge between North and South America; Coates and Obando, 1996. During this mass-dispersal event, mammals (and birds) from North America immigrated and displaced, or filled niches left vacant by South American endemics (Marshall et al., 1982; Stehli and Webb, 1985; Weir et al., 2009). Following immigration, mammals and other biota underwent significant diversification (Webb, 1976; Marshall et al., 1982; Stehli and Webb, 1985; Dacosta and Klicka, 2008). The Pleistocene (c. 2.6–0.011 Ma) represents the ecological aftermath of this intense transformation of South America ecosystems in the context of increasingly fluctuating climates as Earth transitioned into the last Ice Age.

Many recent multidisciplinary studies have sought to reconstruct paleoclimate, paleoenvironment, and faunal biogeography during this ecologically important time. A classic area of focus is the current Mesopotamian region in Argentina (Carlini et al., 2008; Orfeo et al., 2009). The interpretations of paleoenvironmental context in which the Quaternary biota developed, together with detailed faunal analyses performed in the area (Scillato-Yané et al., 1998, 2005; Zurita and Lutz, 2002; Tonni, 2004; Carlini et al., 2003, 2004, 2008; Gasparini and Zurita, 2005; Ferrero and Noriega, 2007; Zurita and Ferrero, 2009, among others) suggest that the northern part of the current Mesopotamian region in Argentina had a biological connection to the southern part of Brazil and western Uruguay, particularly during the wet and warm pulses of the late Pleistocene (Carlini et al., 2003, 2004; Francia and Carlini, 2009). In the past, most of the knowledge of paleoenvironment has come from the study of vertebrates, whereas paleobotanical work has been limited (see Orfeo et al., 2009). The Pleistocene deposits in Mesopotamia consist of two fossil-rich lithostratigraphic units: the

* Corresponding author.
E-mail address: georginaerra@yahoo.com.ar (G. Erra).

1040-6182/$ – see front matter © 2012 Elsevier Ltd and INQUA. All rights reserved.
http://dx.doi.org/10.1016/j.quaint.2012.08.2110

Toropí and Yupoí formations, both representing floodplain sedimentation. Extracted biosilica (phytoliths) from the Toropí and Yupoí formations from a site in the province of Corrientes constitutes the first fossil record of plants in this region. The main objective of this contribution is to analyze these phytolith assemblages to provide a paleoenvironmental interpretation for the late Pleistocene of northeastern Argentina that can be compared to the faunal record in this region.

1.1. Study area: biotas, climates and environments

The Mesopotamian region of Argentina covers 200,000 km^2 between the current Paraná and Uruguay rivers, and includes the territories of Misiones, Corrientes and Entre Ríos provinces (Aceñolaza, 2007). Within Mesopotamia, the Corrientes province covers an area of 88,800 km^2 (Fig. 1). Geomorphologically, the province belongs to a vast sedimentary basin that constitutes a part of ancient shelf relief.

Within the Corrientes province, the area surrounding the town of Bella Vista has a climate described as wet subtropical, characterized by relatively equable temperatures and regular rains throughout the year (Fig. 1). The Mean Annual Temperature (MAT) is 20.9 °C. Soils in the region range from poorly developed over modern sediments to better developed with the formation of A–B–C horizons on top of older material, resulting in Entisols (the least developed soils, on sandy parent material), Mollisols and Alfisols (well developed soils that typically reflect grasslands and forest, respectively) (Herbst and Santa Cruz, 1999). Phytogeographically, the town of Bella Vista is in the Chaco Eastern District (Cabrera, 1976), part of the Mesopotamian parkland. This can be described as a savanna parkland, with mesophyllous, xerophilous and xero-halophilous forests in terrace levels on the river banks and topographic highs, mesophyllous to hygrophilous savannas and abundant weeds in topographic lows, sub-concave plains and sandy ridges, *Syagrus* palm groves in sandy hillocks, a marshy and aquatic vegetation complex, *Copernicia* palm groves and xero-halophilous forests in large depressions of old creeks (Carnevali, 1994).

1.2. Previous approaches: geology and paleontology

1.2.1. Geologic setting and stratigraphy

The geological history of the Quaternary deposits in the province of Corrientes has historically been controversial. Álvarez (1974) initially recognized only one unit for the area, the Yupoí Formation. Based on re-study of fossil vertebrates, minerals from the sand fraction, and clay analysis, Herbst and Álvarez (1977) and Herbst and Santa Cruz (1985) later acknowledged two successive units, the Toropí Formation and the Yupoí Formation, but kept the chronology suggested by Álvarez (1974). More recently, Iriondo (1996) suggested combining the units into a "Toropí/Yupoí Formation" and correlating this new unit to the Hernandarias Formation (Middle Pleistocene, between 0.8 and 1.3 Ma). In contrast, a new analysis of fossil mammals in the area (Scillato-Yané et al., 1998) indicates an age for the sequence (Toropí Formation/Yupoí Formation) comparable to that of the 'Lujanense' *sensu lato*, that is, Middle Pleistocene–Early Holocene (Cione and Tonni, 1995). Finally, recent dating analyses using Optically Stimulated Luminescence (OSL) of the deposits have resulted in ages between 58 ka (for the Toropí Formation) and 36 ka (for the Yupoí Formation), "Lujanense' *sensu strict* (Late Pleistocene–Early Holocene) (Tonni et al., 2005; Tonni, 2007; Carlini et al., 2008). Lithologically, the Toropí Formation is composed of clayey sand, sandy limestone, and sandy clay. The Yupoí Formation consists of pelitic sandstone with variable portions of sandy limestone and sandy clay (Herbst and Santa Cruz, 1999). These units represent floodplain deposits, and are broadly distributed, covering a large part of the western and eastern sections of the Corrientes province along the Paraná and

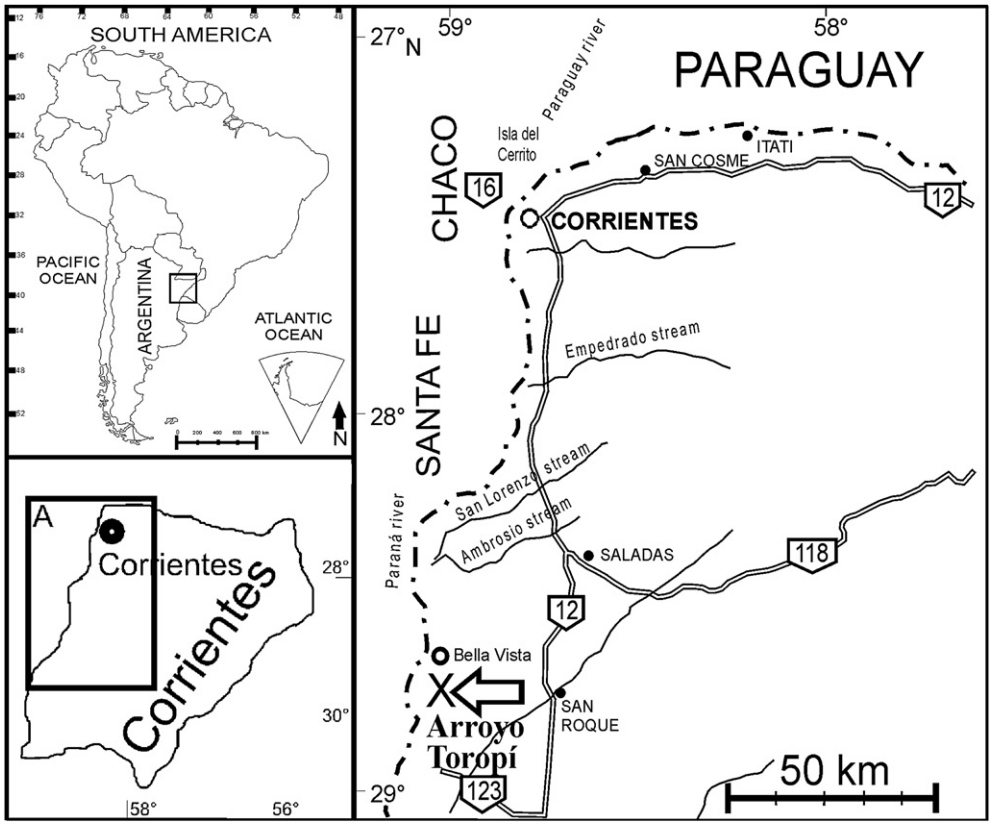

Fig. 1. Location of the Arroyo Toropí locality, Corrientes province, Argentina.

Uruguay rivers, respectively (Herbst and Álvarez, 1975). These Pleistocene units unconformably overlie sandy deposits of the Ituzaingó Formation (Late Miocene–Pliocene), which consist of mineralogically unsorted sands and sporadic, but distinct finer-grained deposits. Both units have broad distributions in Corrientes along the slopes of the Paraná River and distributaries (the Ambrosio Stream, the Santa Lucía River), as well as in some localities along the banks of the Uruguay River and its tributaries, such as the Miriñay (Herbst and Santa Cruz, 1985).

1.2.2. Paleontological evidence

The Toropí and Yupoí formations are both highly fossiliferous (see Herbst, 1971; Iriondo, 1973; Herbst and Álvarez, 1975), and preserve an important and varied fauna of mega- and micro-mammals. The Pleistocene fauna, which has been collected primarily from the outcrops on both margins of the Toropí Colonia Progreso Stream, Department of Bella Vista, is the most diverse fauna found in a single location (see Álvarez, 1974; Scillato-Yané et al., 1998; Zurita and Lutz, 2002; Alcaraz and Carlini, 2003; Carlini et al., 2004; Alcaraz and Francia, 2010; Francia et al., 2010). Invertebrate faunas (pelecypod molluscs, Morton and Jalfin, 1987; Herbst and Santa Cruz, 1999; Morton, 2004) that have recently been described add to the knowledge of the animal communities represented in this unit.

The Late Pleistocene vertebrate faunal record in the province of Corrientes show clear compositional changes through time, linked to fluctuations in climate. Specifically, the changes in diversity are consistent with pulses of colder and arid to semiarid climate (presence of *Stegomastodon platensis*, *Dolichotis* sp., *Pampatherium typum*, *Neosclerocalyptus paskoensis*, *Glyptodon reticulatus,* etc.), alternating with wetter and warmer climate (presence of *Holmesina paulacoutoi*, *Tapirus* sp., *Stegomastodon waringi*, *Euphractus* aff. *sexcintus*, *Boa constrictor*). In this context, species of lineages with more tropical affinities in the 'Lujanense' of the Corrientes province are *H. paulacoutoi*, *S. waringi* and *Tapirus*. Scillato-Yané et al. (2005) associate *H. paulacoutoi* with a wet environment. *Tapirus* is also usually linked to wet to transitional or high altitude forests, particularly near stable bodies of water and fluvial–lacustrine environments (Eisenberg, 1997; Parera, 2002; Ferrero and Noriega, 2007). Finally, *S. waringi* has a clearly tropical distribution (Alberdi et al., 2002). In addition, the great diversity of cervids, including the two rather large *Antifer ultra* and *Antifer ensenadensis* (Alcaraz and Zurita, 2004; Alcaraz and Francia, 2010), suggests diverse environments, with both open areas and trees/shrubs.

Most paleoenvironmental analyses of Pleistocene faunas performed in the Mesopotamian region were conducted on material from the Corrientes and Entre Ríos provinces (Alcaraz and Carlini, 2003; Carlini et al., 2003, 2004, 2008; Noriega et al., 2004; Gasparini and Zurita, 2005; Mino-Boilini et al., 2006; Ferrero et al., 2007; Zurita and Ferrero, 2009; Francia et al., 2009, 2010; Miño-Boilini and Carlini, 2009; Alcaraz and Francia, 2010; Mino-Boilini et al., 2010). Only a few have addressed more in-depth interpretations of paleoclimatology and paleoenvironments (Tonni, 2009). These studies found that Quaternary sediments of the Corrientes province likely reflect successive, frequent environmental fluctuations, resulting in biogeographic ties alternating between the Chaco-Pampean plain and intertropical areas.

The paleobotany of the Cenozoic Mesopotamia is summarized by Anzótegui and Lutz (1985, 1988) and Barreda et al. (2007). The macrofloral record, restricted to a site at the base of the Yupoí Formation in the town of Empedrado, Corrientes, consists of impressions of stems and branches with nodes and internodes with affinities to the current genus *Equisetum* (Lutz and Gallego, 2001). Within Mesopotamia, several studies of phytolith assemblages have been conducted on Neogene deposits of the province of Entre Ríos, namely the marine, middle Miocene Paraná Formation in the Paraná River basin (Zucol and Brea, 2000a, 2000b), the continental, early Pleistocene deposits of the Alvear Formation (Zucol and Brea, 2001, 2005, in press), and the late Pleistocene–Holocene Tezanos Pinto Formation (Kröling et al., 2005; Erra et al., 2006; Erra, 2010a,b, 2011; Erra et al., 2011). In the Uruguay River basin, late Pleistocene phytolith assemblages from a site in the "Parque Nacional El Palmar" of the El Palmar Formation have been analyzed (Zucol and Brea, 2001; Brea et al., 2001a,b; Zucol et al., 2005). In contrast, no work on phytoliths has so far been carried out in the Corrientes province and, given the lack of macrofossils and palynomorphs in the deposits, very little independent evidence for vegetation for this area exists. The goal of this paper is to supply such a paleobotanical record for the late Quaternary of the mid-latitudes of Mesopotamian Argentina and compare it to the associated faunal record, as well as to phytolith assemblages of equivalent age from other formations.

2. Materials and methods

Sections were measured and samples collected for phytolith extraction from the Toropí and Yupoí formations that crop out in the Toropí Stream area (28°36′S, 59°02′W), about 10 km south of the town of Bella Vista, Colonia Progreso, Corrientes province, Argentina (Fig. 1). This stream runs SE–NW, almost at 90° to the course of the Paraná River, into which it flows. It is over 3 km long, with a maximum width of about 500 m (Álvarez, 1974). Two representative profiles, S1 and S2, respectively, were selected, where the remains of two Quaternary mammals, *Lestodon* (Xenarthra, Phyllophaga) (Scillato-Yané et al., 1998) and *Hippocamelus* (Artiodactyla, Cervidae) (Alcaraz, 2010) have previously been excavated. Sedimentological and paleosol descriptions were carried out following standards established by the Soil Survey Staff (1996) (Tables 1 and 2).

Table 1
Description and sedimentological analysis of the sediment in profile S1 ("*Lestodon*").

Sample	Depth (cm)	Color	Structure	Texture	Consistency
M1	7.50–7.20 m	2.5 Y5/2	Structureless	Silt loam	Friable
M2	6.50–6.20 m	5Y6/4	Structureless	Silt loam	Friable
M3	5.50–5.20 m	5Y7/3	Laminar	Silty-clay loam	Friable
M4	4.50–4.20 m	5Y6/4	Laminar	Silty-clay loam	Friable
M5	3.50–3.20 m	5Y6/2	Laminar	Silty-clay	Slightly hard–Slightly adhesive–Slightly plastic
M6	2.50–2.20 m	5Y6/3	Laminar	Silty-clay	Slightly hard–Slightly adhesive–Slightly plastic
M7	1.50–1.20 Hz C	5Y6/2	Laminar	Silt–clay	Very hard–Adhesive–Plastic
M8	0.90–1.20 cm hz Bt3	5Y2/1	Prisms large–Moderate/Strong	Silt–clay	Very hard–Adhesive–Plastic
M9	0.63–0.90 m hz Bt2	5Y5/1	Large–Moderate/Strong Prisms	Silt–clay	Slightly hard–Slightly adhesive–Slightly plastic
M10	0.43–0.63 m hz Bt1	10YR2/2	Medium–Moderate Blocks	Silty-clay	Hard–Adhesive–Plastic
M11	0.30–0.43 m hz AC/B	10YR3/2	Fine–Strong Blocks	Silty-clay	Hard–Adhesive–Plastic
M12	0.15–0.30 m hz A	10YR3/2	Fine–Strong Blocks	Silt loam	Friable
M13	0–0.15 m hz A	10YR4/2	Granular, Fine Weak	Silt loam	Soft, Non adhesive Non plastic
M14	Current soil-Hz A	10YR5/1	Granular, Fine Weak	Silt loam	Soft, Non adhesive Non plastic

Table 2
Description and sedimentological analysis of profile S2 ("*Hippocamelus*").

Sample	Depth (cm)	Color	Structure	Texture	Consistency
M1	2.80 m	5 Y 7/3	Structureless to Granular, fine, weak	Silty sand	Slightly hard–Slightly adhesive–Slightly plastic
M2	2.60 m	5Y 7/4	Fine–Moderate Blocks	Silty loam	Slightly hard–Slightly adhesive–Slightly plastic
M3	2.40 m	5Y 7/2	Granular, medium, Weak	Silty sand loam	Slightly hard–Non adhesive–Non plastic
M4	2.20 m	5Y 7/3	Structureless to Granular, Fine, Weak	Silty clay loam	Friable
M5	2.00 m	5Y 8/4	Structureless to Granular, Fine, Weak	Silty loam	Friable
M6	1.80 m	5Y 8/3	Structureless	Silty clay	Friable
M7	1.60 m	5Y 8/3	Structureless to Granular, Fine, Medium	Silty loam	Friable
M8	1.40 m	5Y 7/3	Structureless	Silty clay	Friable
M9	1.20 m	5Y 7/4	Structureless	Silty loam	Friable
M10	1.00 m	5Y 7/4	Structureless	Silty loam	Slightly hard–Non adhesive–Non plastic
M11	0.80 m	5Y 6/3	Fine–Moderate Blocks	Silty loam	Slightly hard–Non adhesive–Non plastic
M12	0.60 m	5Y 6/3	Medium Moderate Blocks	Silty clay	Slightly hard–Slightly adhesive–Slightly plastic
M13	0.40 m	5Y 6/3	Medium Moderate Blocks	Silty loam	Hard–Slightly adhesive–Slightly plastic
M14	0.20 m	5Y 6/2	Medium Moderate Blocks	Silty loam	Hard–Slightly adhesive–Slightly plastic

Samples were obtained through even sampling from base to top of the sections (Fig. 2). The profiles were cleaned beforehand in order to prevent any contamination. In the S1 ("*Lestodon*") profile (Fig. 2A), the seven lowermost samples were taken every 1 m on average in the Quaternary formations, and the upper seven with decreasing sampling intervals through the modern soil. In all cases, 250 g of sediment was collected. In the espacio S2 ("*Hippocamelus*") profile, 14 samples were taken every 0.20 m (Fig. 2B). All samples ($n = 28$) are curated in the CTES-PB collection of the Facultad de Ciencias Exactas y Naturales y Agrimensura- Universidad Nacional del Nordeste. For the phytolith analysis, 5 g of sample were processed, following a method described by Alvarez et al. (2008). The amorphous silica fraction was separated from the inorganic fraction and concentrated using polytungstate heavy liquid (Alvarez et al., 2008). Phytoliths were mounted on slides in immersion oil, and 500 grains were counted under a Leica optical microscope (DM 2500model) at 400× magnification. Photographs were taken with a Cannon Power Shot S40 digital camera. For identification of different morphotypes, a classification based on the rules and descriptors suggested by Madella et al. (2005) was used. Data processing and graphing were done in POLPAL Numerical Analysis program (Walanus and Nalepka, 1999a, 1999b, 2000; Nalepka and Walanus, 2003). Cluster analyses were carried out using the software Paleontological Statistics (PAST; Hammer et al., 2001).

3. Analyses and results

Twenty-eight samples collected in the field were processed in the laboratory. All contained biosilica (phytoliths, diatoms, sponge spicules etc.) and were therefore included in the analysis. Phytolith assemblages were dominated by morphotypes produced by grasses, including silicified long cells (elongate sinuate, elongate echinate) and short cells, cuneiform bulliform cells (Fig. 4N), and acicular hair cells. Short cell assemblages were characterized by abundant rondels (Fig. 4F), saddles (Fig. 4B) and bilobates (Fig. 4H, J, L). Other morphotypes found include polyhedral epidermis and globular psilate, both commonly produced by dicotyledons (e.g., Bozarth, 1992; Strömberg, 2004), and globular echinate, typical of palms (e.g., Piperno, 1988). The samples are described in more detail below.

3.1. Profile S1 ("Lestodon") description

The Toropí Formation (2.50–7.50 m) in profile S1 (containing specimens of *Lestodon*) is relatively clay-rich, as is typical of this unit, and, as a result, comparatively indurated and with high color chromaticity and value (Table 1, Fig. 2A). The Yupoí Formation (above 2.50 m) is characterized by typical features of the parental materials: argillic endopedons and mollic epipedons. These features of well developed Mollisol and Alfisol paleosols are predominant in these sequences.

3.1.1. Profile S1 biosilica microremains

The amount of silica phytoliths as a weight percentage of the total inorganic component varies between 4.03% and 21.85% through the profile S1 sequence (Fig. 2A). The highest yields were from the modern soil, and the lowest yields from samples from the Yupoí Formation. Apart from phytoliths, other biosilica microremains were found, such as sponge spicules, diatoms, and chrysophyte cysts. The spicules were found in every sample in low frequencies (0.2–1.5%), as were diatoms (0–2%), which reached their maximum amount in the M1 (Toropí Fm.), M12, M13 and M14 (modern soil) samples (2%). Chrysophyte cysts were found exclusively, and always in low abundances (0–4%) in the modern soil samples (M11, M12, M13 and M14).

In general, phytolith assemblages from profile S1 contained the same set of morphotypes, but varied in their relative abundances of these morphotypes through the sequence (Fig. 3). Rondel short cells (Fig. 4E, G) were abundant throughout the section, reaching their highest values in the lower samples (above 40% in M1, M2, M3, M4, M5, M6, M7), and 54% of the phytolith total in M2. Saddles (Fig. 4C) were the next most abundant morphotypes, and decreased from bottom (16.61% in M1) to top (1.17% in M14) in the profile. Conversely, acicular hair cells, cuneiform bulliforms, and elongate sinuate/echinate morphotypes increased towards the top of the section. Acicular hair cells were most frequent in the upper samples (M11, M12, M13, M14), reaching values of 19.00% in M13. Bulliform cells reached their highest abundance in M12 (9.46% of the phytolith total). Elongate sinuate phytoliths (Fig. 4LI), reached 25–30% in M10 and M11 respectively. Other morphotypes that were consistently present include bilobates (Fig. 4D, K), which varied between 6 and 10%, with their highest peaks in M14 (21.23%) and in M3 (17.92%), and elongate psilate (Fig. 4M), with values between 3.26% in M5 and 11.79% in M14. Other rare phytolith morphotypes were pyramidals, globular psilates, globular echinates, polyhedral epidermal cells and square plates, crosses (Fig.4I), silicified vascular (conduction) elements, other plates and irregular elongates. The fraction of unidentified phytoliths was below 2%.

The cluster analysis performed on the unarticulated phytoliths from profile S1 ("*Lestodon*") resulted in three main clusters. The oldest samples in the section (M1–M7) form a cluster that is characterized by relatively high abundances of rondels and saddles and the presence of globular smooth; this group has a 96% similarity (Fig. 3A). The next cluster (M8–M10) has moderately high abundance of rondels, elongate sinuate, and presence of crosses and conduction elements. A cluster containing the youngest

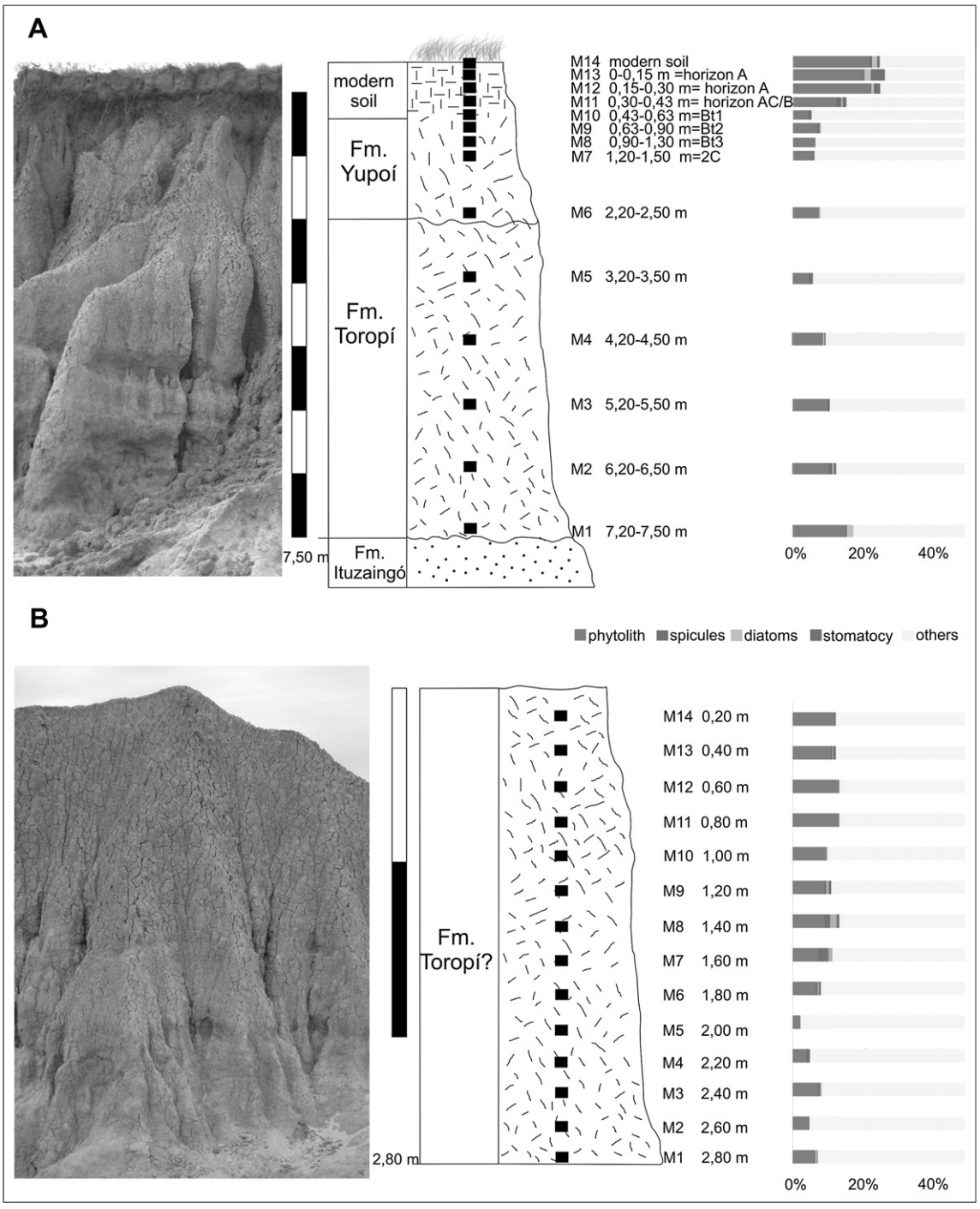

Fig. 2. Diagram and photograph of the profiles from where the phytolith samples were taken, showing the stratigraphic profile from where the micro-morphological samples were taken. A) Profile S1.B) Profile S2.

samples (M11–M14) is typified by low abundance of rondels and saddles, and high abundance of elongate sinuate, cuneiform bulliform cells and acicular hair cells.

3.2. Profile S2 ("Hippocamelus") description

Profile S2, from which the remains of *Hippocamelus* (Artiodactyla, Cervidae) were excavated, is lithologically uniform (Table 2; Fig. 2B). Only in the base of the sequence are olive-colored sediments, more indurated, and have abundant black manganese and iron coatings. Calcium carbonate is found throughout the profile.

3.2.1. Profile S2 biosilica microremains

In profile S2, the percentage of silica phytoliths varies between 2.34% and 12.89% of the total inorganic components (Tables 1 and 2), with the highest values in samples closer to the top of the section. The phytolith morphotypes represented are similar throughout the profile (Fig. 3). The predominant morphotype in all samples is rondel short cells (Fig. 4F), with a maximum of 49% in

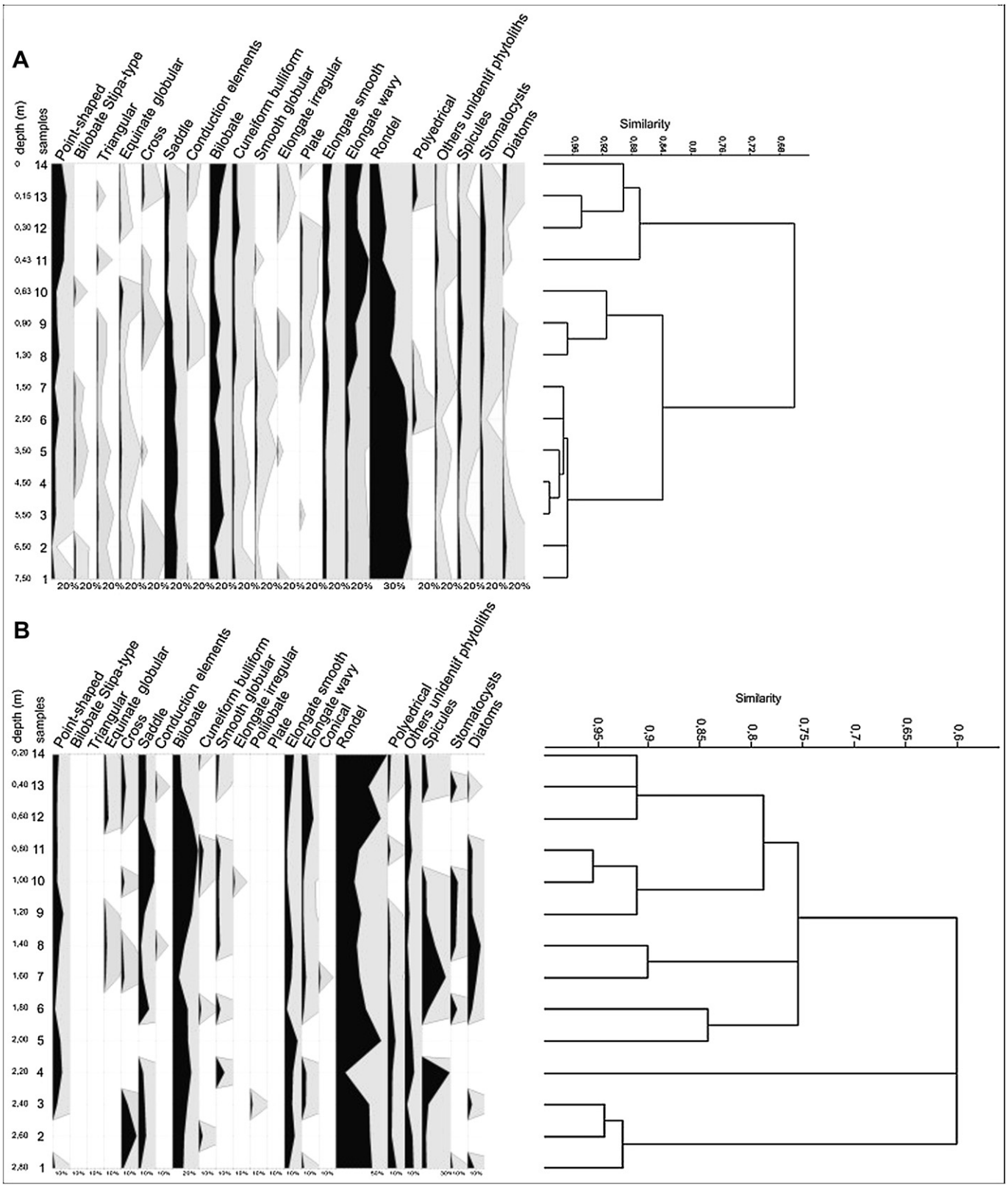

Fig. 3. Phytolith and silica microremains diagram (Polpal program). Abundance of the principal phytolith morphotypes (in quantitative counts). In black: abundance; in gray: exaggeration (factor 5) and cluster analysis (Past program), algorithm paired group, measure similarity Moristia, constrained. A) Profile S1. B) Profile S2.

M14, a minimum value of 8.7% in M4, and varying between 22 and 44% in the rest of the samples. Bilobate short cells(Fig. 4H, J, L) are the second most abundant phytolith type. They range in relative abundance from 7 to28% through the section, with values well above 20% in M9–M11, whereas samples close to the base of the section (M1–M6) have on average ~15% bilobates. Elongate psilates were found in relatively high frequencies, ranging from 2.5% in M11 and M6, to a maximum abundance of 15% in M5 (Fig. 3).

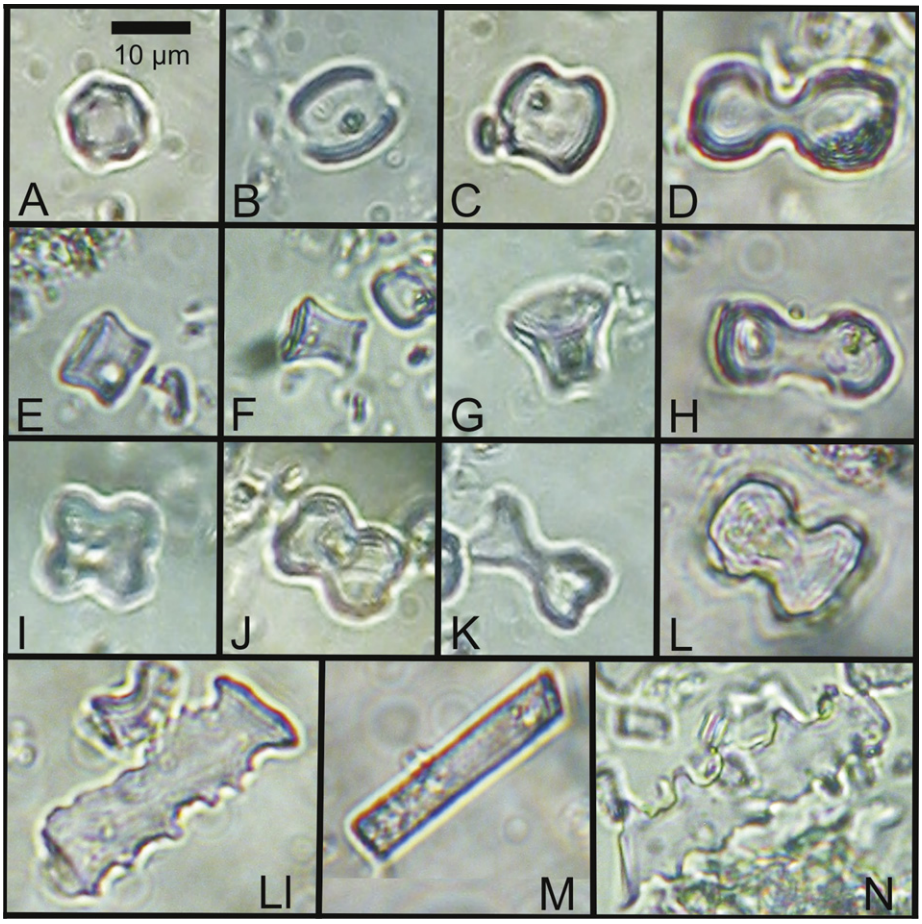

Fig. 4. Isolated phytoliths. A) globular echinate from profile S2.B) saddle from profile S2. C) saddle from profile S1. D, K) bilobates from profile S1. E, G) rondels from profile S1. F) rondel from profile S2. H, J, L) bilobates from profile S2.I) cross from profile S1. LI, M) elongate from profile S1. N) elongate from profile S2.

Acicular hair cell, cross, saddle, polyhedral epidermis, cuneiform bulliform, and elongate sinuate/echinate types were found in all samples, but in low relative abundances (Fig. 3). Globular psilate and globular echinate (Fig. 4A) were found in very low frequencies.

The cluster analysis performed on the phytolith assemblages from ProfileS2 ("*Hippocamelus*") clustered 90% of samples, resulting in one smaller cluster of the oldest samples (M1–M3) and a larger cluster containing all other samples but one (M4) (Fig. 3B). The latter group is subdivided into four smaller clusters. The oldest cluster has predominantly rondels, abundant elongate psilate, low frequencies of elongate psilate and saddles, and no acicular hair cells, a cluster with M7 and M8 is typified by the presence of bilobates, rondels, acicular hair cells, and low abundances of saddles and cuneiform bulliform cells, the second to youngest cluster (M9–M11) has lower frequencies of rondels and elongate sinuate, and relatively high abundances of bilobates and saddles, and the youngest cluster (M12–M14) is characterized by abundant rondels and elongate sinuate, and the presence of acicular hair cells and cuneiform bulliform cells.

4. Discussion

Changes in vegetation in South America during the Miocene and the Pliocene are thought to have been influenced by the progressive decline in global temperatures and the increase in aridity, likely linked with several factors such as the rise of the Andes, changes in oceanic and atmospheric circulation, the development of the Antarctic ice-sheet, the continental–ocean relation and ongoing Andean volcanism (Coira et al., 1982; Barreda et al., 2007). During the Pleistocene Ice Age, the alternation of glacial and interglacial periods had a profound influence on the distribution and composition of vegetation. Both climatic variability and the high frequency in climatic shifts imposed a unique stress on the biota and caused isolation of communities, reduction and fragmentation of habitats and impoverishment of floras established during the Paleogene and Neogene (Markgraf and McGlone, 2006). Previous work has shown that Anacardiaceae, minosoid Fabaceae, and palm forests may have developed in wet and warm-temperate conditions during the EI 5 interglacial period (Barreda et al., 2007).

The paleobotanical record, including phytolith assemblages, representing the Pleistocene in the Mesopotamia differs from the Miocene record (e.g., Barreda et al., 2007). Although the same taxa (e.g., palms, different grass subclades) seem to have persisted in the region into the Quaternary, relative abundance composition and, hence, vegetation structure of the floras varied; this variation appears to be tied to different fluvial facies of the rivers Paraná and Uruguay. For example, Erra (2010a) described phytolith assemblages from formations coeval with the Toropí and Yupoí formations in the Argentinean Mesopotamia (e.g., Tezanos Pinto Formation, Entre Ríos province) that indicate open grazing land with an abundant palm trees. The grass community reflected in these assemblages was made up mainly of panicoids and chloridoids mixed with pooids, particularly stipoids, forming a mesothermal community (*sensu* Burkart, 1975); the associated palms

and sedges further indicate wet conditions (e.g., Uhl and Dransfield, 1987; Strömberg, 2004; Piperno, 2006).

The phytolith records from the Corrientes region indicate that open, grass-dominated communities developed in fluvial–lacustrine environments in Argentinean Mesopotamia by the middle Pleistocene. Based on changes in composition through profile S1, these grass-dominated habitats were initially dominated by non-stipoid pooid grasses (producing rondels) with a lower but consistent contribution from chlorioid grasses (producing saddles). Further up section, in particular in the modern soil, these grass lineages appeared to have become slightly less abundant, resulting in a relatively higher contribution from potential panicoid grasses [or other grasses within the PACMAD (Panicoideae, Arundinoideae, Chloridoideae, Micrairoideae, Aristidoideae, Danthonioideae; Aliscioni et al., 2012) clade producing bilobates and crosses], which remains moderately abundant through the section. Profile S2, which covers an interval of time corresponding to the base of profile S1, shows no consistent change in relative abundances of grass subclades but is consistent with profile S1 in reflecting high abundances of pooids and moderate abundances of chlorioids and panicoids. Relatively even, low frequencies of palms, and low to high frequencies of diatoms, sponge spicules and chrysophyte cysts through the sections suggest habitats close to water; low abundances of morphotypes indicative of woody and herbaceous dicotyledonous angiosperms indicate that the vegetation included a few trees or shrubs.

Because particular grass subclades tend to be associated with different climatic conditions, the phytolith assemblages can also shed light on climate during the Pleistocene of the Argentinean Mesopotamia. Specifically, the Pooideae subfamily C_3 grasses that tend to dominate cool-temperate or high-elevation grasslands, the Chloridoideae subfamily contain grasses with C_4 photosynthetic pathway found in warm and arid climates, and the Panicoideae subfamily, are either C_3 or C_4 and generally from tropical or subtropical regions (Twiss, 1992; Kellogg, 2001; Edwards and Smith, 2010). The mix of pooids, chloridoids, and potential panicoids should point to a relatively warm, semi-arid climate.

Thus, the phytolith data and information from the associated mammalian fauna suggest that the climate in the Mesopotamian region was very different from that inferred for the Pampean region, central-northern Argentina, Paraguay, and southern Bolivia. In the Chaco-Pampean plains climate is thought to have been relatively cold and arid during the Pleistocene (Tonni et al., 1999). In contrast, for at least the main part of the Pleistocene, the Mesopotamian region would have had a more humid and warmer climate, with a marked influence from Brazilian climatic conditions, that would have continued even during the second-to-last interglacial period (Scillato-Yané et al., 2002; Carlini et al., 2004).

5. Conclusion

Phytolith assemblages associated with mammalian faunas from the Pleistocene Toropí and Yupoí formations in Argentinean Mesopotamia were analyzed. All the analyzed samples showed a predominance of grass phytoliths, with a low frequency of morphotypes from forest indicator taxa. Grass phytolith assemblages were dominated by forms produced in abundance by C_3 pooid grasses, but also contained moderate frequencies of phytoliths typical of C_4 espacio chlorioids and C_3 or C_4 panicoids (or other PACMAD grasses). This mix of C_3 and C_4 grasses indicate relatively warm and dry climates. However, the relatively consistent presence of palm phytoliths and non-plant biosilica wetland indicators (diatoms, sponges, chrysophyte cysts) point to a riparian element on the landscape. This reconstructed climate and vegetation—grasslands with groves of palms and other trees of shrubs—are consistent with paleoenvironmental interpretations based on faunas recovered from the same sediments. It also fits well with work dating the sediments to between 58 ka and 36 ka (within MIS 3). Based on these lines of evidence, frequent climatic-environmental variations during the Late Pleistocene led to a fluctuation in biogeographic connections between the Mesopotamian region and other parts of South America. During certain times, Mesopotamia would have been more closely linked to the Chaco-Pampean plain and, during other times, to inter-tropical regions. This may have influenced the development of mesothermal, grass-dominated ecosystems (*sensu* Burkart, 1975), formed by a mix of C_3 and C_4 grasses, which today inhabit mainly warm-temperate regions.

Acknowledgements

This research has been financially supported (PICTO 07/164 to AAC, and UNMdP, project 15/E 551/2011) to MO. We thank C.A.E. Strömberg for helping improve the manuscript.

References

Aceñolaza, F.G., 2007. Geología y Recursos Geológicos de la Mesopotamia Argentina. Serie de Correlación Geológica 22, 149.

Alberdi, M.T., Cartelle, C., Prado, J.L., 2002. El registro de *Stegomastodon* (Mammalia, Gomphotheriidae) en el Pleistoceno superior de Brasil. Revista Española de Paleontologia 17 (2), 217–235.

Alcaraz, M.A., Carlini, A.A., 2003. Los cérvidos (Mammalia, Artiodactyla) de las Formaciones Toropí y Yupoí (Pleistoceno medio-tardío) de la provincia de Corrientes, Argentina. Comunicaciones Científicas y Tecnológicas de la Universidad Nacional del Nordeste. Corrientes Versión on line sin paginación. http://www.unne.edu.ar.

Alcaraz, M.A., Francia, A., 2010. Diversidad de Cervidos (Mammalia, Artiodactyla) durante el Pleistoceno de la provincia de Corrientes, Argentina. In: XXIII Jornadas Argentinas de Mastozoología. Universidad Nacional del Sur, Bahía Blanca. Libro de resúmenes, p. 41.

Alcaraz, M.A., Zurita, A.E., 2004. Nuevos registros de cérvidos poco conocidos: *Epieuryceros cf. proximus Castellanos y Antifersp. (Mammalia, Artiodactyla, Cervidae)*. Revista del Museo Argentino de Ciencias Naturales, n.s. 6 (1), 41–48.

Alcaraz, M.A., 2010. Sistemática de los Cérvidos (Mammalia, Artiodactyla) del Pleistoceno de las áreas extraandinas de Argentina. Tesis de Doctoral Inédita, Universidad Nacional de La Plata, 302 pp.

Aliscioni, S., Bell, H.L., Besnard, G., Christin, P.A., Columbus, J.T., Duvall, M.R., Edwards, E.J., Giussani, L., Hasenstab-Lehman, K., Hilu, K.W., Hodkinson, T.R., Ingram, A.L., Kellogg, E.A., Mashayekhi, S., Morrone, O., Osborne, C.P., Salamin, N., Schaefer, H., Spriggs, E., Smith, S.A., Zuloaga, F., 2012. New grass phylogeny resolves deep evolutionary relationships and discovers C4 origins. New Phytologist 193, 304–312.

Álvarez, B.B., 1974. Los mamíferos fósiles del Cuaternario de Arroyo Toropí, Corrientes, Argentina. Ameghiniana 11, 295–311.

Alvarez, M.F., Borrelli, N., Osterrieth, M., 2008. Extracción de silicofitolitos en distintos sedimentos utilizando dos técnicas básicas. In: Korstanje, M.A., Babot, M. del P. (Eds.), Matices Interdisciplinarios en Estudios Fitolíticos y de Otros Microfósiles, pp. 31–38. BAR International Series S1870.3.

Anzótegui, L., Lutz A., 1985. Paleocomunidades vegetales de la Formación Ituzaingó (Plioceno) de la Mesopotamia Argentina. Resúmenes: V Reunión de Paleobotánicos y Palinólogos, Sao Paulo, Brazil.

Anzótegui, L., Lutz, A., 1988. Paleocomunidades del Terciario Superior (Formación Ituzaingó) de la Mesopotamia Argentina. Revista de la Asociación de Ciencias Naturales del Litoral 18 (2), 134–144.

Barreda, V., Anzótegui, L.M., Prieto, A.R., Aceñolaza, P., Bianchi, M.M., Borromei, A.M., Brea, M., Caccavari, M., Cuadrado, G.A., Garralla, S., Grill, S., Guerstein, G.R., Lutz, A.I., Mancini, M.V., Mautino, L.R., Ottone, E.G., Quattrocchio, M.E., Romero, E.J., Zamaloa, M.C., Zucol, A., 2007. Diversificación y cambios de las angiospermas durante el Neógeno en Argentina. Ameghiniana 11, 173–191. 50° aniversario. Publicación Especial.

Bozarth, S.R., 1992. Classification of opal phytoliths formed in selected dicotyledons native to the Great Plains. In: Rapp, G.J., Mulholland, S.C. (Eds.), Phytolith Systematics. Emerging Issues. Advances in Archaeological and Museum Science. Plenum Press, New York, pp. 193–214.

Brea, M., Zucol, A.F., Scopel, A., 2001a. Estudios paleobotánicos del Parque Nacional El Palmar (Argentina). I. Presencia de cuerpos de sílice en leños fósiles de Mirtaceae. Natura Neotropicalis 32 (1), 33–40.

Brea, M., Zucol, A.F., 2001b. Estudio paleobotánico del Parque Nacional El Palmar (Entre Ríos, Argentina): Silicobiolitos en sedimentos continentales del Pleistoceno Superior. Ameghiniana 38 (4-suplemento), 29R. Buenos Aires.

Burkart, A., 1975. Evolution of grasses and grasslands in South America. Taxon 24, 53–66.

Cabrera, A.L., 1976. Regiones Fitogeográficas Argentinas: Enciclopedia Argentina de Agricultura y Jardinería, Segunda edición, Tomo II, 85 pp.
Carlini, A.A., Zurita, A.E., Gasparini, G.M., Noriega, J.I., 2003. Los mamíferos del Pleistoceno de la Mesopotamia argentina y su relación tanto con aquellos del Centro-Norte de la Argentina, Paraguay, sur de Bolivia, como con los del sur de Brasil y oeste de Uruguay: Paleobiogeografía y Paleoambientes. Revista del Instituto Superior de Correlación Geología (Misceláneas) 12, 5–12.
Carlini, A.A., Zurita, A.E., Gasparini, G., Noriega, J.I., 2004. Los mamíferos del Pleistoceno de la Mesopotamia argentina y su relación con aquéllos del Centro-Norte de la Argentina, Paraguay y Sur de Bolivia, Sur de Brasil y Oeste de Uruguay: Paleobiogeografía y Paleoambientes. In: Aceñolaza, F.G. (Ed.), Temas de la Biodiversidad del Litoral fluvial argentino, pp. 83–90. INSUGEO, Miscelánea, 12.
Carlini, A.A., Zurita, A.E., Miño-Boilini, A.R., 2008. Reseña paleobiogeográfica de los Xenarthra (Mammalia) del Pleistoceno tardío de la región Mesopotámica (Argentina). INSUGEO Miscelánea 17 (2), 259–270.
Carnevali, R., 1994. In: Fitogeografía de la Provincia de Corrientes. Gobierno de la Provincia de Corrientes e Instituto Nacional de Tecnología Agropecuaria (INTA). Editora Litocolor S. R. L., Paraguay, pp. 1–324.
Cione, A.L., Tonni, E.P., 1995. Chronostratigraphy and "Land-Mammal Ages" in the Cenozoic of Southern South America: principles, practices, and the "Uquian" problem. Journal of Paleontology 69 (1), 135–159.
Coates, A.G., Obando, J.A., 1996. The geologic evolution of the Central American Isthmus. In: Jackson, J.B.C., Budd, A.F., Coates, A.G. (Eds.), Evolution and Environment in Tropical America. University of Chicago Press, Chicago, pp. 21–56.
Coira, B., Davidson, J., Mpodozis, C., Ramos, V., 1982. Tectonic and magmatic evolution of the Andes of northern Argentina and Chile. Earth-Science Reviews 18, 303–332.
Dacosta, J.M., Klicka, J., 2008. The Great American Interchange in birds: a phylogenetic perspective with the genus *Trogon*. Molecular Ecology 17, 1328–1343.
Eisenberg, J.F., 1997. Introduction. In: Brooks, D.M., Bodmer, R.E., Matola, S. (Eds.), Tapirs-status Survey and Conservation Action Plan, vol. viii. IUCN, Gland, Switzerland and Cambridge.
Edwards, E.J., Smith, S.A., 2010. Phylogenetic analyses reveal the shady history of C4 grasses. Proceedings of the National Academy of Sciences USA 107, 2532–2537.
Erra, G., 2010a. Estudio fitolítico de la Formación Tezanos Pinto (Pleistoceno Tardío-Holoceno Temprano) en la provincia de Entre Ríos, Argentina. Tesis doctoral FCNyM, U.N.L.P., 277 pp.
Erra, G., 2010b. Asignación sistemática y paleocomunidades inferidas a partir del estudio fitolítico de sedimentos cuaternarios de Entre Ríos, Argentina. Boletín de la Sociedad Argentina de Botánica 45 (3–4), 309–319.
Erra, G., 2011. Criterios metodológicos para el estudio y clasificación de fitolitos cuaternarios. Revista Historia Natural. Tercera Serie 1, 45–62.
Erra, G., Zucol, A.F., Kröhling, D., Brea, M., 2006. Análisis fitolíticos en el loess del Pleistoceno Tardío–Holoceno Temprano en la provincia de Entre Ríos: resultados preliminares. In: III Congreso Argentino de Cuaternario y Geomorfología, Actas de trabajo, tomo II, pp. 691–699:13.
Erra, G., Zucol, A.F., Kröhling, D.M., 2011. Análisis fitolítico de la Formación Tezanos Pinto (loess del Pleistoceno Tardío- Holoceno Temprano) en el sector noroeste de su área de distribución en la provincia de Entre Ríos (Argentina). Revista Mexicana de Ciencias Geológicas 28 (3), 398–412.
Ferrero, B., Brandoni, D., Noriega, J.I., Carlini, A., 2007. Mamíferos de la Formación El Palmar (Pleistoceno tardío) de la provincia de Entre Ríos, Argentina. Revista del Museo Argentino de Ciencias Naturales, n.s. 9 (2), 109–117.
Ferrero, B.S., Noriega, J.I., 2007. A new tapir from the Upper Pleistocene of Argentina: phylogenetic remarks on the Neotropical family diversification and paleoenvironmental inferences. Journal of Vertebrate Paleontology 27 (2), 504–511.
Francia, A., Carlini, A.A., Zurita, A.E., 2009. Novedades acerca de Mamíferos cuaternarios del ArroyoToropí, Corrientes: sus implicancias biogeográficas. Reunión de comunicaciones científicas y tecnológicas vol. 2009, Corrientes. Versión on line sin paginación CB-029 (http://www.unne.edu.ar).
Francia, A., Zurita, A.E., Carlini, A.A., 2010. Diversidad de Cingulata (Mammalia, Xenarthra) en el Pleistoceno tardío de la provincia de Corrientes (Argentina) y dinámica paleoclimática. Reunión de Comunicaciones Científicas y Tecnológicas 2010, Corrientes. Libro de resúmenes on-line CB-068.
Francia, A., Carlini, A.A., 2009. La fauna del Pleistoceno tardío de Corrientes (Mesopotamia, Argentina), su relevancia paleobiogeográfica. In: 3° Jornadas de Jóvenes Investigadores, La Plata, Bs. As. Libro de resúmenes en CD. ISBN: 978-950-34-0593-2.
Gasparini, G.M., Zurita, A.E., 2005. Primer registro fósil de *Tayassupecari* (Link) (Mammalia, Artiodactyla) en la Argentina. Ameghiniana 42, 473–480.
Hammer, O., Harper, D.A.T., Ryan, P.D., 2001. Past-palaeontological Statistics, ver. 1.75, 86 pp.
Herbst, R., Alvarez, B.B., 1975. Nota sobre dos Formaciones del Cuaternario en Corrientes. Anales de la Academia Brasilera de Ciencias 47 (Suppl.), 33–37.
Herbst, R., Álvarez, B.B., 1977. Nota sobre dos formaciones del Cuartario de Corrientes, República Argentina. FACENA 1, 7–17.
Herbst, R., Santa Cruz, J.N., 1985. Mapa litoestratigráfico de la provincia de Corrientes. D'Orbignyana 1, 1–50.
Herbst, R., Santa Cruz, J.N., 1999. Mapa litoestratigráfico de la provincia de Corrientes. D'Orbignyana 2, 1–69.
Herbst, R., 1971. Esquema estratrigrafico de la provincia de Corrientes. Revista de la Asociación Geológica Argentina XXVI (2), 221–243.
Iriondo, M.H., 1973. Mineralogía de las arenas de la Formación Yupoi. Revista de la Asociación de Ciencias Naturales del Litoral 4, 87–96.
Iriondo, M.H., 1996. Estratigrafía del Cuaternario de la cuenca del río Uruguay. In: Actas XIII Congreso Geológico Argentino y III Congreso de Exploración de Hidrocarburos, vol. 4, pp. 15–25.
Kellogg, E.A., 2001. Evolutionary history of the grasses. Plant Physiology 125, 1198–1205.
Kröling, D., Zucol, A.F., Brea, M., Aguirre, M.L., Passeggi, E., 2005. Resultados preliminares de estudios sedimentológicos y paleobiológicos de la Formación Tezanos Pinto (Cuaternario) en el SO de Entre Ríos. In: IV Taller de Sedimentología y Medio Ambiente. AAS, CECOAL (CONICET), UNNE: 6–8. Corrientes.
Lutz, A., Gallego, O., 2001. Nuevos hallazgos fosilíferos (vegetales e icnofósiles) en el cuaternario de la provincia de Corrientes. Reunión de comunicaciones de la Asociación Paleontológica Argentina. Ameghiniana: 36R.
Madella, M., Alexandre, A., Ball, T., 2005. International code for phytolith nomenclature 1.0. Annals of Botany 96, 253–260.
Markgraf, V., McGlone, M., 2006. Southern temperate ecosystem responses. In: Lovejoy, T.E., Hannah, L. (Eds.), Climate Change and Biodiversity. Yale University Press, New Haven, pp. 142–156.
Marshall, L.G., Webb, S., Sepkoski Jr., J., Raup, D., 1982. Mammalian evolution and the great American interchange. Science 215, 1351–1357.
Morley, R.J., 2003. Interplate dispersal paths for megathermal angiosperms. Perspectives in Plant Ecology Evolution and Systematics 6, 5–20.
Mino-Boilini, A.R., Cerdeño, E., Bond, M., 2006. Revisión del género *Toxodon* Owen, 1837 (Notoungulata: Toxodontidae) en el Pleistoceno de las provincias de Corrientes, Chaco y Santa Fe, Argentina. Revista Española de Paleontologia 21 (9), 93–103.
Mino-Boilini, Ángel R., Zurita, Alfredo E., Francia, Analía, Bond, Mariano, 2010. Sobre un supuesto Haplodontheriinae Kraglievich, 1934 (Mammalia, Toxodontidae) en el Pleistoceno tardío de la provincia de Corrientes (Argentina). Reunión de Comunicaciones Científicas y Tecnológicas 2010, Corrientes. Libro de resúmenes on-line CB-003.
Miño-Boilini, A.R., Carlini, A.A., 2009. The Scelidotheriinae Ameghino, 1904 (Phyllophaga, Xenarthra) from the Ensenadan-Lujanian Stage/Ages (Early Pleistocene to Early-Middle Pleistocene-Early Holocene) of Argentina. Quaternary International 210, 93–101.
Morton, L.S., Jalfin, A.G., 1987. Análisis de la Formación Ituzaingó en la localidad de Empedrado y alrededores, provincia de Corrientes, Argentina. Hallazgo del género Mycetopoda (M. herbsti nov. sp.) y revisión de la malacofauna asociada con algunas consideraciones paleoecológicas. FACENA 7, 207–221.
Morton, S.L., 2004. Moluscos fósiles de agua dulce de la Formación Ituzaingó, Plioceno de Corrientes, Argentina. Revista del Insugeo (Misceláneas) 12, 45–48.
Nalepka, D., Walanus, A., 2003. Data processing in pollen analysis. Acta Palaeobotanica 43, 125–134.
Noriega, J.I., Carlini, A.A., Tonni, E.P., 2004. Vertebrados del Pleistoceno tardío de la cuenca del Arroyo Ensenada (Departamento Diamante, Provincia de Entre Ríos). Revista del Instituto Superior de Correlación Geología (Misceláneas) 12, 71–77.
Orfeo, O., Parsons, D., Best, J., Lutz, A.I., Zurita, A.E., 2009. The Paraná River: from Pleistocene to the Present. In: 9th International Conference on Fluvial Sedimentology. F.G. Aceñolaza (Coordinador-Editor). IIESGLO, Miscelánea, vol. 17(2), pp. 259–270.
Parera, A., 2002. Los mamíferos de Argentina y la región austral de Sudamérica. Editorial El Ateneo, Buenos Aires, Argentina, 458 pp.
Piperno, D.R., 1988. Phytolith Analysis, an Archaeological and Geological Perspective. Academic Press, San Diego.
Piperno, D.R., 2006. Phytoliths: a Comprehensive Guide for Archaeologists and Paleoecologists. AltaMira Press, New York.
Ricklefs, R.E., 2002. Splendid isolation: historical ecology of the South American passerine fauna. Journal of Avian Biology 33, 207–211.
Scillato-Yané, G.J., Carlini, A.A., Tonni, E.P., Noriega, J.I., 2005. Paleobiogeography of the Late Pleistocene Pampatheres of South America. Journal of South American Earth Sciences 20 (1–2), 131–138.
Scillato-Yané, G.J., Tonni, E.P., Carlini, A.A., Noriega, J.I., 1998. Nuevos Hallazgos de Mamíferos del Cuaternario en el Arroyo Toropí, Corrientes, Argentina. Aspectos Bioestratigráficos, Paleoambientales y Paleozoogeográficos. In: Actas X Congreso Latinoamericano de Geología y VI Congreso Nacional de Geología Económica (1): pp. 263–268.
Scillato-Yané, G.J.; Carlini, A.A.; Tonni, E.P., Noriega, J.I., Kemer, R., 2002. *Holmesina paulacoutoi*, un pampaterio septentrional y la importancia de su registro en el Cuaternario de la Mesopotamia Argentina. In: 8° Congreso Argentino de Paleontología y Bioestratigrafía, Resúmenes: 54.
Simpson, G.G., 1980. Splendid Isolation, the Curious History of South American Mammals. Yale University Press, New Haven.
Soil Survey Staff, 1996. Keys to Soil Taxonomy, seventh ed. United States Department of Agriculture, Washington D.C, 644 pp.
Stehli, F.G., Webb, S.D., 1985. Great American Biotic Interchange. Plenum Press, New York.
Strömberg, C.A.E., 2004. Using phytolith assemblages to reconstruct the origin and spread of grass-dominated habitats in the Great Plains during the late Eocene to early Miocene. Palaeogeography, Palaeoclimatology, Palaeoecology 207, 239–275.
Tonni, E.P., Cione, A.L., Figini, A.J., 1999. Predominance of arid climates indicated by mammals in the pampas of Argentina during the Late Pleistocene and Holocene. Palaeogeography, Palaeoclimatology, Palaeoecology 147, 257–281.
Tonni, E.P., 2009. Las unidades portadoras de vertebrados del Cuaternario de las regiones Mesopotámica y Pampeana Oriental de la Argentina. Ensayo de correlación. In: Ribeiro, Bauermann, Scherer (Eds.), Cuaternario do Rio Grande do

Sul. Integrando conocimientos. Monografías da Sociedade Brasileira de Paleontología, pp. 57–66.
Tonni, E.P., Carlini, A.A., Zurita, A., Frechen, M., Gasparini, G., Budziak, D., Kruck, W., 2005. Cronología y bioestratigrafía de las unidades del Pleistoceno aflorantes en el arroyo Toropí, provincia de Corrientes, Argentina. In: XIX Congresso Brasileiro de Paleontología y VI Congresso Latino-Americano de Paleontología, resumos (vers. electrónica).
Tonni, E.P., 2004. Faunas y clima en el Cuaternario de la Mesopotamia argentina. In: Aceñolaza, F.G. (Ed.), Temas de la biodiversidad del litoral fluvial argentino, pp. 31–38. Instituto Superior de Correlación Geológica, Miscelánea, 12.
Tonni, E.P., 2007. Mamíferos del Cuaternario de laregión Pampeana. Workshop de Quaternário Do RS "Integrando conhecimentos". Libro de Resúmenes, Canoas, Brazil, pp. 48–50.
Twiss, P.C., 1992. Predicted world distribution of C3 and C4 grass phytoliths. In: Rapp Jr., G., Mulholland, S.C. (Eds.), Phytolith Systematics: Emerging Issues. Advances in Archaelogical and Museum Science, vol 1, pp. 113–128.
Uhl, N.W., Dransfield, J., 1987. Genera Palmarum. Allen Press, Lawrence, Kansas.
Walanus, A., Nalepka, D., 1999a. POLPAL. Program for counting pollen grains, diagram plotting and numerical analysis. Acta Palaeobotanica (Suppl. 2), 659–661.
Walanus, A., Nalepka, D., 1999b. POLPAL. Numerical Analysis. W. Szafer Institute of Botany. Polish Academy of Sciences, Polonia, pp. 1–10.
Walanus, A., Nalepka, D., 2000. POLPAL. Counting Pollen, Tables Storage and Diagrams Plotting. System Manual. W. Szafer Institute of Botany. Polish Academy of Sciences, Polonia, pp. 1–25.
Webb, S.D., 1976. Mammalian faunal dynamics of the great American interchange. Paleobiology 2, 220–234.
Weir, J.T., Bermingham, E., Schluter, D., 2009. The great American biotic interchange in birds. Proceedings of the National Academy of Sciences of the United States of America 106, 21737–21742.
Zucol, A.F., Brea, M., 2000a. Análisis fitolítico de la Formación Paraná en la provincia de Entre Ríos. In: Aceñolaza, G., Herbst, R. (Eds.), El Neógeno de Argentina, pp. 67–76. Serie Correlación Geológica, 14.
Zucol, A.F., Brea, M., 2000b. Análisis fitolítico de la Formación Paraná (Mioceno superior) en el Departamento Diamante, Entre Ríos, Argentina. In: II Congreso Sedimentológico Latinoamericano y VIII Reunión Argentina de Sedimentología, Resúmenes: pp. 190–191, Mar del Plata.
Zucol, A.F., Brea, M., 2001. Asociación fitolítica de la Formación Alvear (Pleistoceno Inferior), Entre Ríos, Argentina. Ameghiniana 38 (4-suplemento), 49R. Buenos Aires.
Zucol, A.F., Brea, M., 2005. Sistemática de fitolitos, pautas para un sistema clasificatorio. Un caso en estudio en la Formación Alvear (Pleistoceno inferior). Ameghiniana 42 (4), 685–704.
Zucol, A.F., Brea, M. Asociación fitolítica de la Formación Alvear (Pleistoceno inferior), Entre Ríos, Argentina. In: Zucol, A.F., Osterrieth, M.L., Brea, M. (Eds.), Fitolitos en suelos, sedimentos y sitios arqueológicos: Estado actual de sus conocimientos en América del Sur. Mar del Plata, in press.
Zucol, A.F., Brea, M., Scopel, A., 2005. First record of fossil wood and phytolith assemblages of the Late Pleistocene in El Palmar National Park (Argentina). Journal of South American Earth Sciences. ISSN: 0895-9811 20. ISSN: 0895-9811, 33–43.
Zurita, A.E., Ferrero, B., 2009. Una nueva especie de Neuryurus Ameghino (Mammalia, Glyptodontidae) en el Pleistoceno tardío de la Mesopotamia de Argentina. Geobios 42, 663–673.
Zurita, A.E., Lutz, A.I., 2002. La fauna pleistocena de la Formación Toropí en la provincia de Corrientes (Argentina). Mastozoología Neotropical 9, 47–56.