Palaeoenvironment associated with giant tortoises of Toropí/Yupoí Formation (Late Pleistocene 50–28 ka), Corrientes province, Argentina

L. Fernandez Pacella[a,*], G.G. Zacarías[b], M. Di Pasquo[c]

[a] Centro de Ecología Aplicada del Litoral (CECOAL-CONICET-UNNE), Dpto. Biología - FaCENA-UNNE, Ruta 5, Km 2,5, CC 128, 3400, Corrientes, Argentina
[b] Cátedra de Vertebrados, Facultad de Ciencias Naturales, Carrera de Ingeniería en Recursos Naturales y Medio Ambiente, Universidad Nacional de Salta, Sede Regional Orán, Alvarado 751, 4530, Salta, Argentina
[c] Laboratorio de Palinoestratigrafía y Paleobotánica, CICyTTP-CONICET, Dr. Materi & España S/n, Diamante, E3105BWA, Entre Ríos, Argentina

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ABSTRACT

Vertebrate faunas of the Mesopotamian region in Argentina provided palaeoclimatic and palaeoenvironmental information from the Pleistocene. Samples collected into a carapace of the turtle *Chelonoidis lutzae* and associated sediments obtained from the Toropí/Yupoí Formation (Arroyo Toropí, Bella Vista) palynologically studied for the first time. The palynomorph association includes angiosperms (Brassicaceae, Amaranthaceae, Poaceae, Sapotaceae, Fabaceae, Euphorbiaceae, Myrtaceae), Bryophyta, Pteridophyte (*Microgramma squamulosa*), chlorophytes (*Pediastrum tetras, Botryococcus*) and fungal spores (*Dichomera, Phaeoseptoria* sp., *Phragmotrichum* sp., *Agaricus* sp.). Palaeoecologic requirements of these botanical groups indicate the predominance of herbaceous palaeocommunities associated with arboreal or shrubby elements and fresh waters bodies. They characterized dynamic scenarios typical of ecotonal zones under arid/semi-arid and humid warm seasonal climates during the Late Pleistocene (Last Maximum Glacial) in the Mesopotamian region.

1. Introduction

Many recent multidisciplinary studies have attempted to reconstruct palaeoenvironment and faunistic biogeography during the Pleistocene, and the Mesopotamian region of Argentina is ideal because fossiliferous Quaternary deposits are dominant (Carlini et al., 2008; Orfeo et al., 2009; Erra et al., 2013, among others). Modern studies suggest that the Mesopotamian region (Entre Ríos, Corrientes and Misiones provinces), was differentiated from the Pampas region and north-central Argentina, at least during a large part of the Pleistocene based on palaeofaunistic and palaeoenvironmental characteristics. A biological connection of northern Mesopotamia with southern Brazil and western Uruguay was established during the humid and warm pulses of the Late Pleistocene (Ubilla et al., 2004; Francia and Carlini, 2009). This was supported on detailed studies of vertebrate faunas (e.g. Scillato-Yané et al., 1998; Carlini et al., 2008; Tonni, 2004; Zurita and Ferrero, 2009; Erra et al., 2013, among others).

Mammals represent most of the palaeontological records of the Pleistocene of Corrientes province whereas contributions on Palaeobotany are scarce (Lutz and Gallego, 2001; Erra et al., 2013). Fossil pollen data from chronologically constrained sedimentary sequences is widely used to reconstruct the history of vegetation and infer

changes of climatic conditions. Our contribution aims to present the first palynologic study of the sediments associated with carapace of the giant tortoises *Chelonoidis lutzae* (Zacarías et al., 2013) found in the Lower Member of the Toropí/Yupoí Formation exposed in the town of Bella Vista, Corrientes province (Fig. 1).

2. Geological, stratigraphic and palaeoenvironmental context

The holotype of *Chelonoidis lutzae* (Testudinidae) preserved dorsal shell, plastron and remains of the appendicular skeleton (Zacarías et al., 2014) was extracted from the upper section of lower member of the Toropí/Yupoí Formation of Arroyo Toropí (Fig. 1). This unit is distributed along the eastern margin of Paraná River overlying the Ituzaingó Formation (Late Miocene, ca. 7-2 Ma - Present *sensu* Iriondo, 2010). Initially, Herbst (1971) named this unit as Yupoí Formation, dividing it into two members. Subsequently, Herbst and Álvarez (1974) used fossil mammals to divide this unit in two formations, Toropí [e.g. *Theriodictis* sp. and *Scelidodon* sp. (Floor/Age: Ensenadense sensu Pascual et al., 1965)] and Yupoí [*Megatherium* sp., *Euphractus* sp. and *Equus* sp. (Floor/Age: Lujanense sensu Pascual et al., 1965)]. However, such division based on mammalian biochrones did not hold in later studies because their ranges (biochron) were extended (Ubilla et al.,
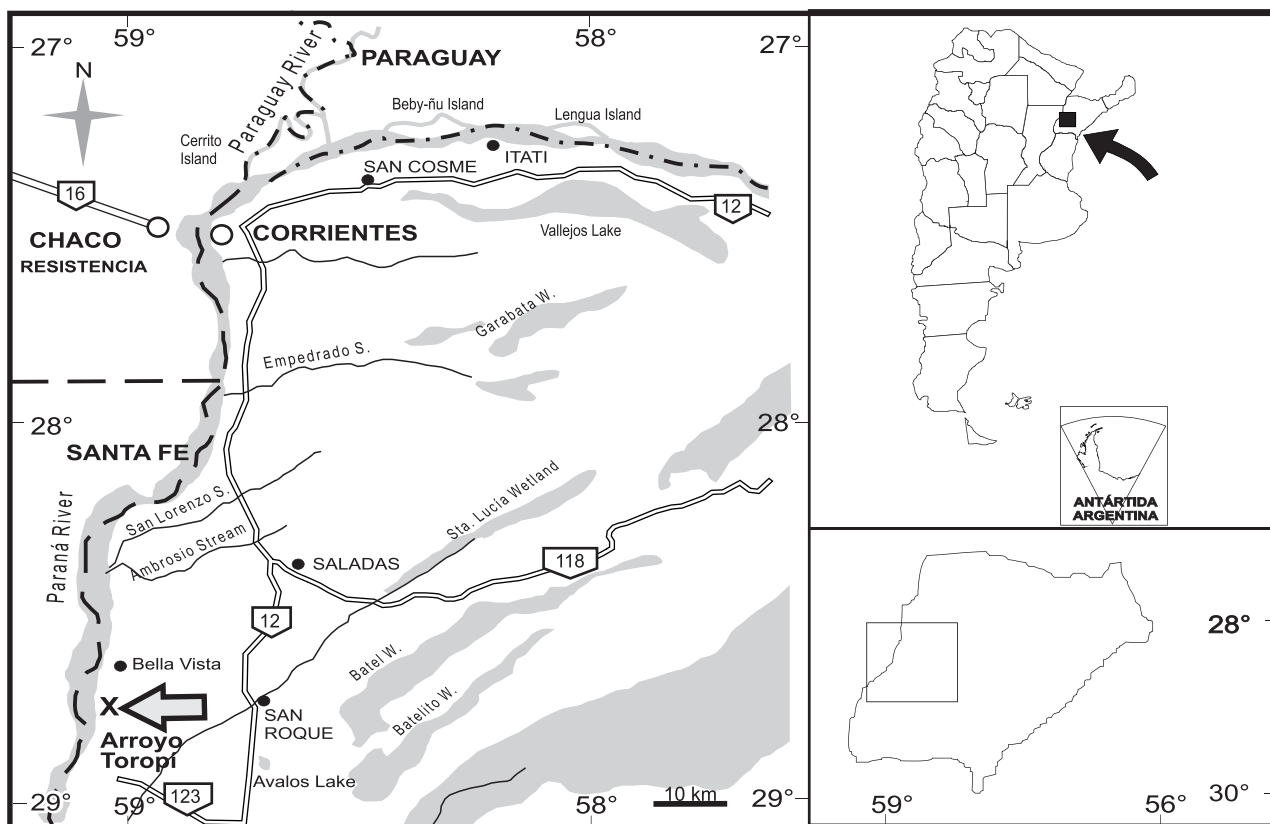
Fig. 1. Geographic map of Corrientes province, the arrow indicates the fossiliferous locality (Taken and modified from Zacarías et al., 2013).

2004; Cione and Tonni, 2005; Carlini et al., 2008; Francia et al., 2012, among others). On the other hand, Iriondo (2010) and Iriondo and Kröhling (2008) postulated that both formations are the same through mineralogical analysis, so to avoid confusion, we use the composite term Toropí/Yupoí in agreement with Herbst (1971) are used.

The Toropí/Yupoí Formation is composed of clayey sands, sandy silts and sandy clays in variable proportions (Herbst, 1971). Two informal members are recognized: the lower one is composed of yellow to green massive sandstone strata separated from the upper member by a thin layer (surface) of very compacted sandstone called "siliceous crust" (*sensu* Scillato-Yané et al., 1998). In turn, less consolidated sediments characterize the upper member with a greater lithological variety and colors, from pink to red, differentiating in some areas two sections, in which the upper one is darker. In Arroyo Toropí, Herbst (1971) uses the "siliceous crust" to mark the limit between the lower and upper members (Fig. 2).

Optically Stimulated Luminescence analysis (OSL) of the Toropí/Yupoí Formation suggests that it was deposited during 58–28 Ka (Late Pleistocene), correlated with the MIS 3 (Oxigen Marine Isotope Stages) (Francia et al., 2012). It is important to note that during MIS 3, the Paraná River was located in a more eastern position than today, possibly occupying the paleochannels of the Aguapey and Miriñay Rivers, in contact with the Uruguay River (Iriondo and Kröhling, 2008; Iriondo, 2010).

Palaeoclimatic and palaeoenvironmental differences proposed for the Yupoí and Toropí formations by different authors. Different hypothesis postulated for the Yupoí and Toropí formations as independent units. One interpretation (1a) considered arid cold environments for the Toropí Formation and, warmer and humid for the Yupoí Formation (Herbst and Álvarez, 1974). A second one (2a) established for the Toropí Formation arid/cold and warm/humid lapses based on palaeoenvironmental requirements of the vertebrate fauna (Scillato-Yané et al., 1998; Carlini et al., 2008; Francia et al., 2012, among others).

The third one (3a) supported warm and humid conditions with marked seasonality, and low to moderate levels of saturation of water availability in well-developed soils with abundant vegetation for both formations based on the phytolithic analysis from termite mounds and sediments (Erra et al., 2013). Two hypotheses for the Toropí/Yupoí Formation as the same stratigraphic unit proposed: (1b) warm and humid conditions (Iriondo, 2010; Iriondo and Kröhling, 2008, among others; (2b) dynamic ecotonal palaeoenvironment influenced by palaeoclimatic changes (Francia et al., 2012; Zacarías et al., 2014).

On the other hand, high concentrations of clays montmorillonites and illites with respect to the kaolinites found in this unit (Herbst and Santa Cruz, 1985) support complex climatic conditions with well-marked seasons of semi-arid and humid and temperate periods. Montmorillonites form in seasonal semi-arid condition and illites under cold or very dry and kaolinites in humid and temperate climates (Iriondo, 2007). This mineralogical evidence is congruent with three of the previous palaeoclimates and palaeoenvironmental hypotheses (3a), (1b) and (2b). In turn, abundance of fern *Equisetum* sp. in upper member of Toropí/Yupoí Formation supports warm and humid environmental conditions (Lutz and Gallego, 2001). Currently, this genus lives in sandy-clayey soils with high levels of water saturation and subjected to periods of flooding (Husby, 2009). Zacarías et al. (2014) suggest that *Ch. lutzae* is a Neotropical taxon related to the Chaco phytogeographic province that would have lived in more humid environments.

3. Materials and methods

The preparation and cleaning of the holotype of *Chelonoidis* allowed the collection of six mud-limestone samples (5–10 grs.) from the space between the carapace and plastron. In addition, four samples from the upper section of lower member of the Toropí/Yupoí Formation associated with the *Chelonoidis* carapace (28°31′20.24″S-59°03′34.91″W)
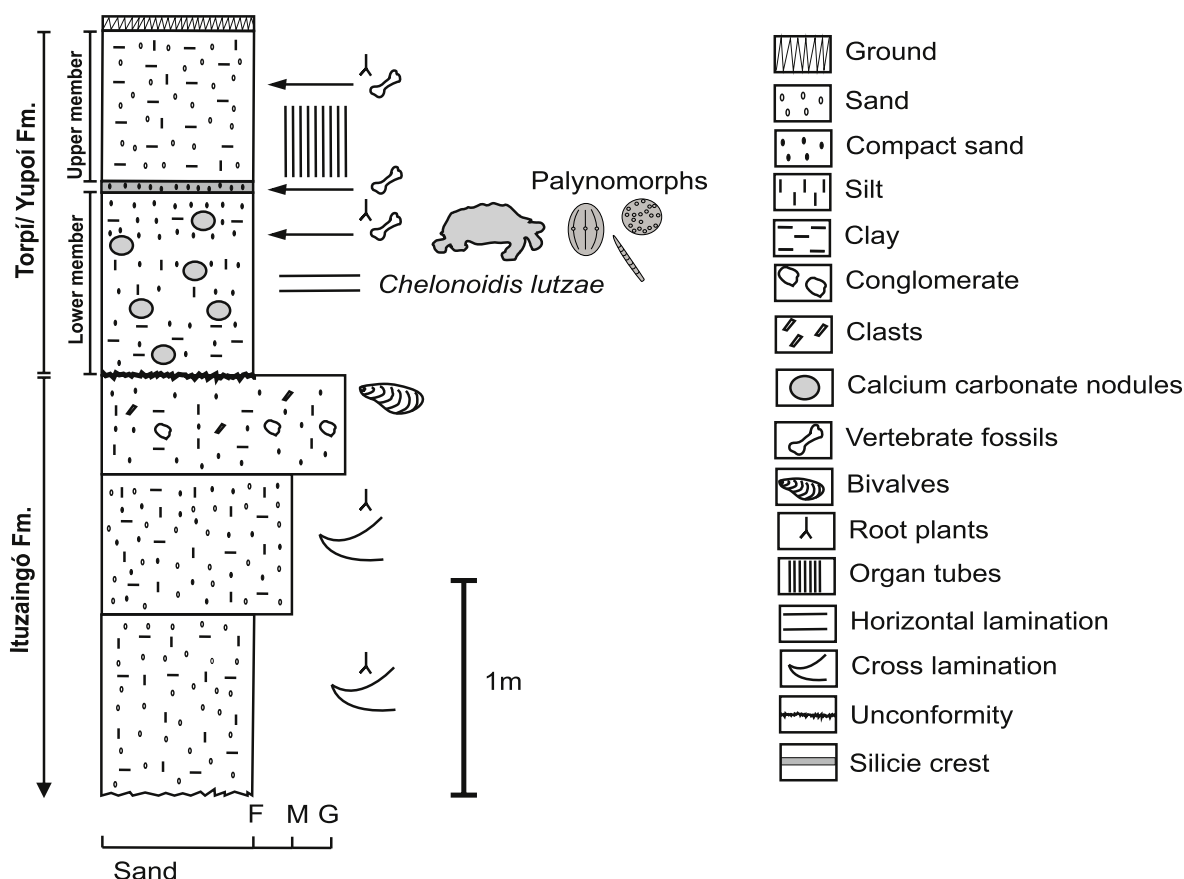
Fig. 2. Stratigraphic profile elaborated from the lithological descriptions of Herbst (1971) and Iriondo (2010) (Taken and modified from Zacarías et al., 2013).

obtained. The samples were processed applying HCl (10%) and HF (52%) to eliminate carbonates, silica and silicates. A mixture of 25 cc sodium chlorate (NaClO$_3$, 80% of concentration), 75 cc acetic acid (CH$_3$COOH) and 6 cc of concentrated sulfuric acid (H$_2$SO$_4$) used to oxidize organic matter. The elimination of humates was performed using dilute alkalis (Heusser and Stock, 1984). After each stage, successive washes with distilled water in centrifuge were done and were sieved with 10–40-100 μm meshes and slides mounted with jelly-glycerin. This procedure was carried out at the laboratory of CECOAL (Centro de Ecología Aplicada del Litoral)-CONICET (Consejo Nacional de Investigaciones Científicas y Tecnológicas)-UNNE (Universidad Nacional del Nordeste), and samples are housed in the collection "Dr. Rafael Herbst" under the acronym PMP-CTES.

The analysis of the samples was made using an optical microscope Nikon Eclipse E100 and palynomorphs were illustrated with a camera Nikon 590CU (40× and 100× magnification and 13 Mp). We followed the classification of Curtis et al. (2001) for pollen grains, and Genus included in the APG III Classification System (2009). The terminology used for descriptions of pollen grains and spores is that of Punt et al. (2007) and contributions of Sáenz Laín (2004), and Nilson and Praglowski (1992) were consulted. The identification of pollen grains, spores and algae was achieved using the reference collection PAL-CTES of the UNNE and specialized literature (Markgraf & D'Antoni, 1978; Boelcke, 1992; Barnett and Hunter, 1998; Salazar Allen, 2011; Oliva-Martínez et al., 2014, among others). In order to establish the paleoenvironment of the fossil pollen paleocommunities, the vegetation of the studied area is used as a modern analogue. To obtain relative frequencies of pollen taxa, the total number of specimens per slide was count up to achieve ca. 250 and represented in pollen diagrams according to ecological requirements using the Tilia- Tilia Graph and TGView 2.0.2 (Grimm, 2004).

4. Systematic paleontology

The samples yielded fairly well preserved species of angiosperms (6), ferns (1), bryophytes (1) fungal and algal remains (Fig. 3) and the main groups of taxa described following the order in Plates I and II.

Kingdom PLANTAE Haeckel, 1866.
Division MAGNOLIOPHYTA Cronquist et al., 1966.
Class MAGNOLIOPSIDA http://www.tropicos.org/Person/989 Brongniart, 1843.
Order BRASSICALES Bromhead, 1838.
Family BRASSICACEAE Burnett, 1835.
Genus *Rorippa* Scopoli, 1760.
Rorippa bonariensis Macloskie, 1905 (Plate I, A; B).

Description: prolate-spheroidal pollen grain, radial symmetry, isopolar, trilobate amb, tricolpate, diameter 14–21 μm. Colpus up to 3.8–4 μm wide. Exine semi-tectated, 1.8–2.2 μm thick. Reticulate, heterobrochate, lumens decrease their diameter towards the poles.

Main studied material: PMP-CTES. N°: 3612.

Comparisons: to reach our determination, the specimens were compared with *Rorippa bonariensis* (Salgado and Pire, 1996), subsequently included within *Rorippa clandestina* Type (Salgado and Pire, 1998) present in the extant flora of Corrientes.

Order CARYOPHYLLALES Jussieu ex Berchtold & Presl, 1820
Family AMARANTHACEAE Jussieu, 1789.
Subfamily AMARANTHOIDEAE Schinz, 1893
Genus *Amaranthus* Linnaeus, 1753
Amaranthus muricatus Hieronymus, 1882 (Plate I C; D).

Description: spheroidal pollen grain, radial symmetry, apolar, pantoporate, diameter 22 μm. Circular pores, operculated, pore numbers 30 distributed in all surface of grain, 1.2 μm diameter. Exine tectated, 1.1 μm thick, on tectum positive elements distributed densely on surface of grain. Microechinate.
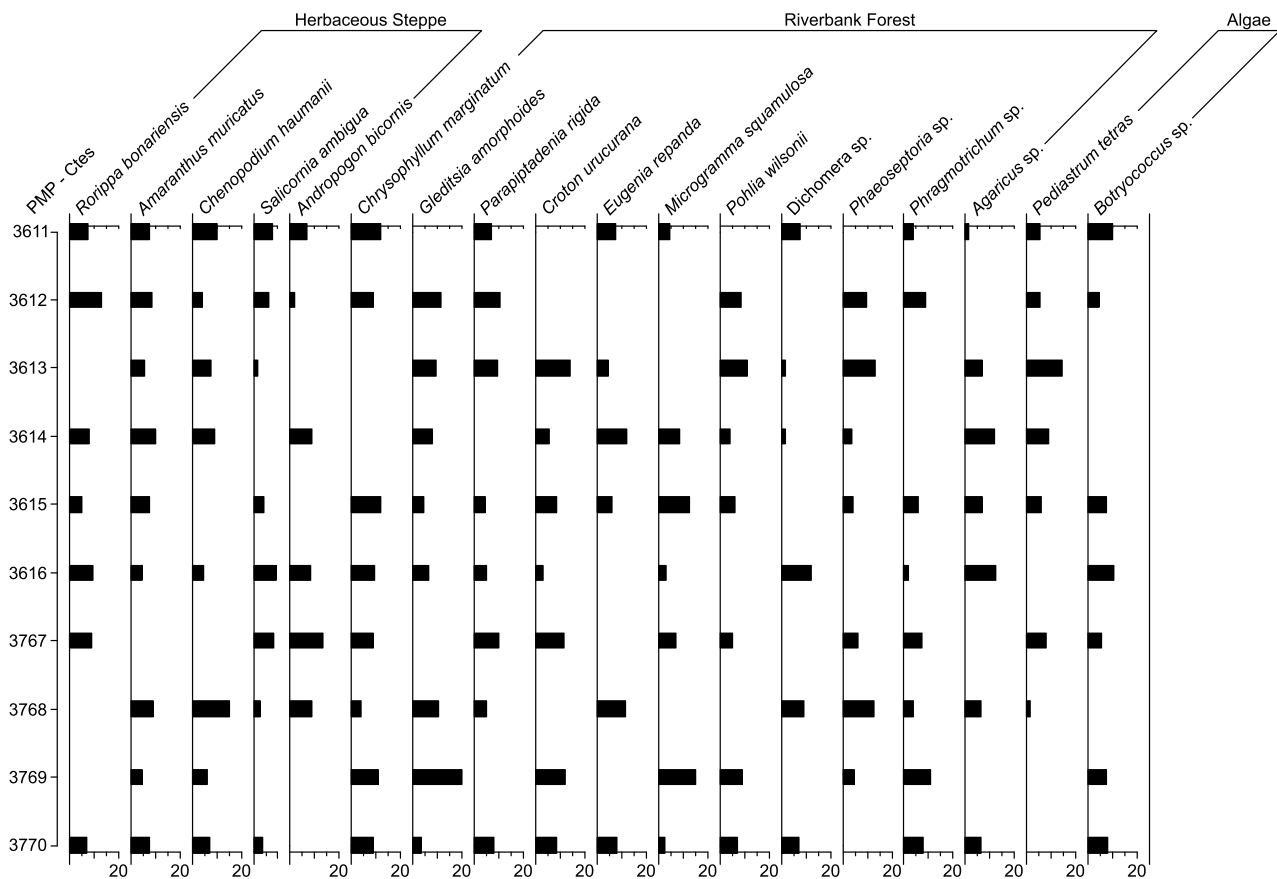
Fig. 3. Palynological percentage diagram of the samples analyzed.

Main studied material: PMP-CTES. Nº: 3767; 3770.

Comparisons: to reach our determination, the specimens were compared with *Amaranthus muricatus* Subtype (Cuadrado, 1998a) present in the extant flora of Corrientes.

Subfamily CHENOPODIOIDEAE Burnett, 1835

Genus *Chenopodium* Linnaeus, 1753

Chenopodium haumanii Ulbrich, 1934 (Plate I, E; F).

Description: spheroidal pollen grain, radial symmetry, apolar, pantoporate, diameter 17–19 μm. Circular pores, operculated, pore numbers 98–103 distributed in all surface of grain, 0.7–1 μm diameter. Exine tectated, 1.7–1.9 μm thick, on tectum positive elements distributed densely on surface of grain. Microechinate.

Main studied material: PMP-CTES. Nº: 3611.

Comparisons: the specimens were compared with *Chenopodium haumanii* (Cuadrado, 1993), subsequently included within *Holombergia tweedii* Type (Cuadrado, 1998b) present in the extant flora of Corrientes.

Genus *Salicornia* Linnaeus, 1753

Salicornia ambigua Michaux, 1803 (Plate I, G-I).

Description: spheroidal pollen grain, radial symmetry, apolar, pantoporate, diameter 21–23 μm. Circular pores, operculated; number of pores ± 87, distributed in all surface of grain, 1.9–2 μm in diameter. Exine tectate, 1.7–2 μm thick. Microerchinate.

Main studied material: PMP-CTES. Nº: 3611.

Comparisons: the morphology of our specimens agree with *Salicornia ambigua* described by Cuadrado (1993, 1998b) present in the extant flora of Corrientes.

Order ERICALES Berchtold & Presl, 1820

Family SAPOTACEAE Jussieu, 1789

Genus *Chrysophyllum* Linnaeus, 1753

Chrysophyllum marginatum (Hooker & Arnott) Radlkofer, 1887 (Plate I, J-L).

Description: prolate pollen grain, radial symmetry, isopolar, tetracolporate, polar axis 20–24 μm, equatorial axis 14–16 μm. Narrow colpi ± 13.5 μm long. Lalongate pores 1.5 × 2.8 μm with an annular thickening of endexine. Exine 2.6 μm thick, columellary infratectal layer is observed. Slightly rugulate.

Main studied material: PMP-CTES. Nº: 3769; 3770.

Comparisons: the specimens were compared with *Chrysophyllum marginatum* Type (Cuadrado, 1998c) present in the extant flora of Corrientes.

Order FABALES Bromhead, 1838.

Family FABACEAE Lindley, 1836.

Subfamily CAESALPINIOIDEAE de Candolle, 1825.

Tribe CAESALPINIEAE Reichenbach, 1832.

Genus *Gleditsia* Clayton, 1753.

Gleditsia amorphoides (Grisebach) Taubert, 1892 (Plate I, M-P).

Description: subspheroidal to prolate pollen grain 31.5–32.8 × 28.3–30.6 (polar axis x equatorial axis), radial symmetry, isopolar, subtriangular amb, 3–colporate. Long and narrow colpi (6–7.4 μm wide). Lalongate pores 1.6–3.5 x 3–4.2 μm (equatorial axis x polar axis). Semitectate exine 2.8–4 μm thick. Heterobrochate reticulate.

Main studied material: PMP-CTES. Nº: 3768.

Comparisons: to reach our determination, the specimens were compared with *Gleditsia amorphoides* Type (Fernandez Pacella et al., 2013) present in the extant flora of Corrientes.

Subfamily MIMOSOIDEAE de Candolle, 1825.

Tribe MIMOSEAE Bronn, 1822.

Genus *Parapiptadenia* Brenan, 1963.

Parapiptadenia rigida (Bentham) Brenan, 1963 (Plate II, A).

Description: subcircular polyad of 32.3 × 30.1 μm, formed by 16 pollen grains. Pseudocolpus parallel to distal face of grains. Number of pores 4–5. Areolated exine 0.9–1 μm thick.
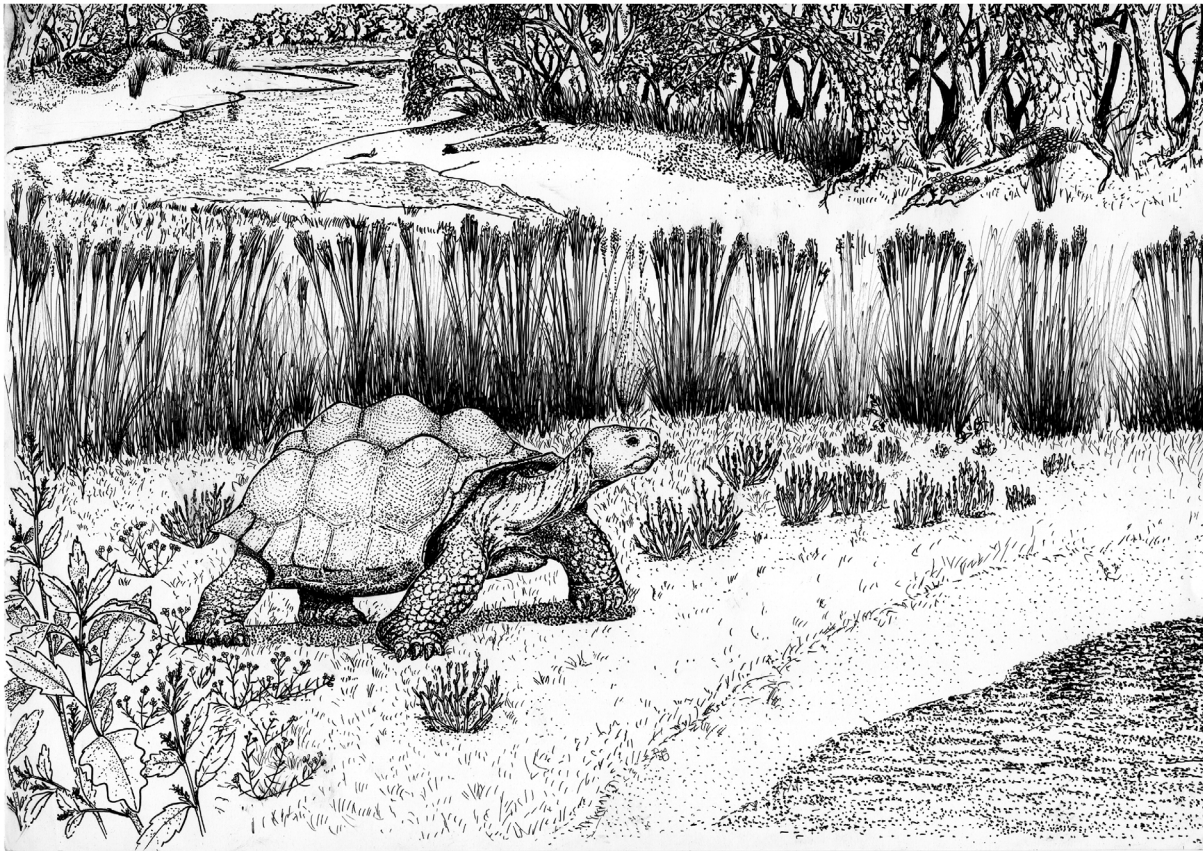
Fig. 4. Palaeoenvironmental reconstruction inferred for *Chelonoidis lutzae*.

Main studied material: PMP-CTES. Nº: 3612; 3613.

Comparisons: the specimens are morphologically equal to *Parapiptadenia rigida* Type described in the extant flora of Corrientes (Caccavari and Dome, 2006).

Order MALPIGHIALES Jussieu ex Berchtold & Presl, 1820.
Family EUPHORBIACEAE Jussieu, 1789.
Subfamily CROTONOIDEAE Burmeister, 1837.
Tribe CROTONEAE Dumortier, 1829.
Genus *Croton* Linnaeus, 1753.
Croton urucurana Baillon, 1864 (Plate II, B-D).

Description: spheroidal pollen grain, diameter 54.7–63.3 μm, radial symmetry, apolar, inaperturate. Exine tectate, gemmate (croton pattern), exine thickness 3.9–4.3 μm (including gems).

Main studied material: PMP-CTES. Nº: 3770.

Comparisons: the morphology of our specimens agree with *Croton urucurana* (Silva et al., 2014).

Order MYRTALES Jussieu ex Berchtold & Presl, 1820.
Family MYRTACEAE Jussieu, 1789.
Subfamily MYRTOIDEAE Sweet, 1827.
Tribe MYRTEAE de Candolle, 1827.
Genus *Eugenia* Linnaeus, 1753.
Eugenia repanda Berg, 1857 (Plate II, E-G).

Description: 3-colporate pollen grain, radial symmetry, isopolar, small size 15.8–17.3 μm. Triangular amb, straight sides. Lineal colpi. Pores 2.5–3. Exine 1.7–2 μm thick. Rugulate.

Main studied material: PMP-CTES. Nº: 3767; 3769.

Comparisons: the specimens were compared with *Eugenia burkartiana* Subtype (Acevedo and Anzótegui, 1998) present in the extant flora of Corrientes.

Class LILIOPSIDA Batsch, 1802.
Order CYPERALES Hutchinson, 1934.
Family POACEAE Barnhart, 1895.

Subfamily PANICOIDEAE Horaninow, 1847.
Tribe ANDROPOGONEAE Dumortier, 1824.
Genus *Andropogon* Linnaeus, 1753.
Andropogon bicornis Forsskal, 1775 (Plate II, H).

Description: subspheroidal pollen grain, radial symmetry, heteropolar, monoaperturate, 31–34 μm in diameter. Ulcus 1.7–2.6 μm diameter with an ectexine ring of 2.2–3.8 μm thick. Exine 1.2–1.8 μm thick, tectate, psilate.

Main studied material: PMP-CTES. Nº: 3611; 3614.

Comparisons: our specimens are in agreement with the morphology of this species described in the extant flora of Corrientes (Fernandez Pacella and Canteros, 2013).

Division MONILOPHYTA Smith et al., 2006.
Class PTERIDOPSIDA Ritgen, 1828.
Order POLYPODIALES Link, 1833.
Family POLYPODIACEAE Presl & Presl, 1822
Genus *Microgramma* Presl, 1836.
Microgramma squamulosa (Kaulfuss) de la Sota, 1961 (Plate II, I).

Description: spore monolete of bilateral symmetry, distal face convex in equatorial view. Polar axis 27–32 μm, equatorial axis 40–67 μm. Lesurae 32–58 μm length. Exospore verrucate, the warts are enlarged towards the distal face in radial disposition. Sporoderm 1.3–2 μm thick.

Main studied material: PMP-CTES. Nº: 3614; 3615.

Comparisons: our specimens agree with the description of *Microgrammas quamulosa* published by Lorscheistter et al. (2005).

Division BRYOPHYTA Schimper, 1879
Pohlia wilsonii (Mitten) Ochyra, 2008 (Plate II, J).

Description: vegetative protection structures, brown, pluricellular, ellipsoidal, flattened; measures 60–75 × 37–58 μm.

Main studied material: PMP-CTES. Nº: 3612; 3613.

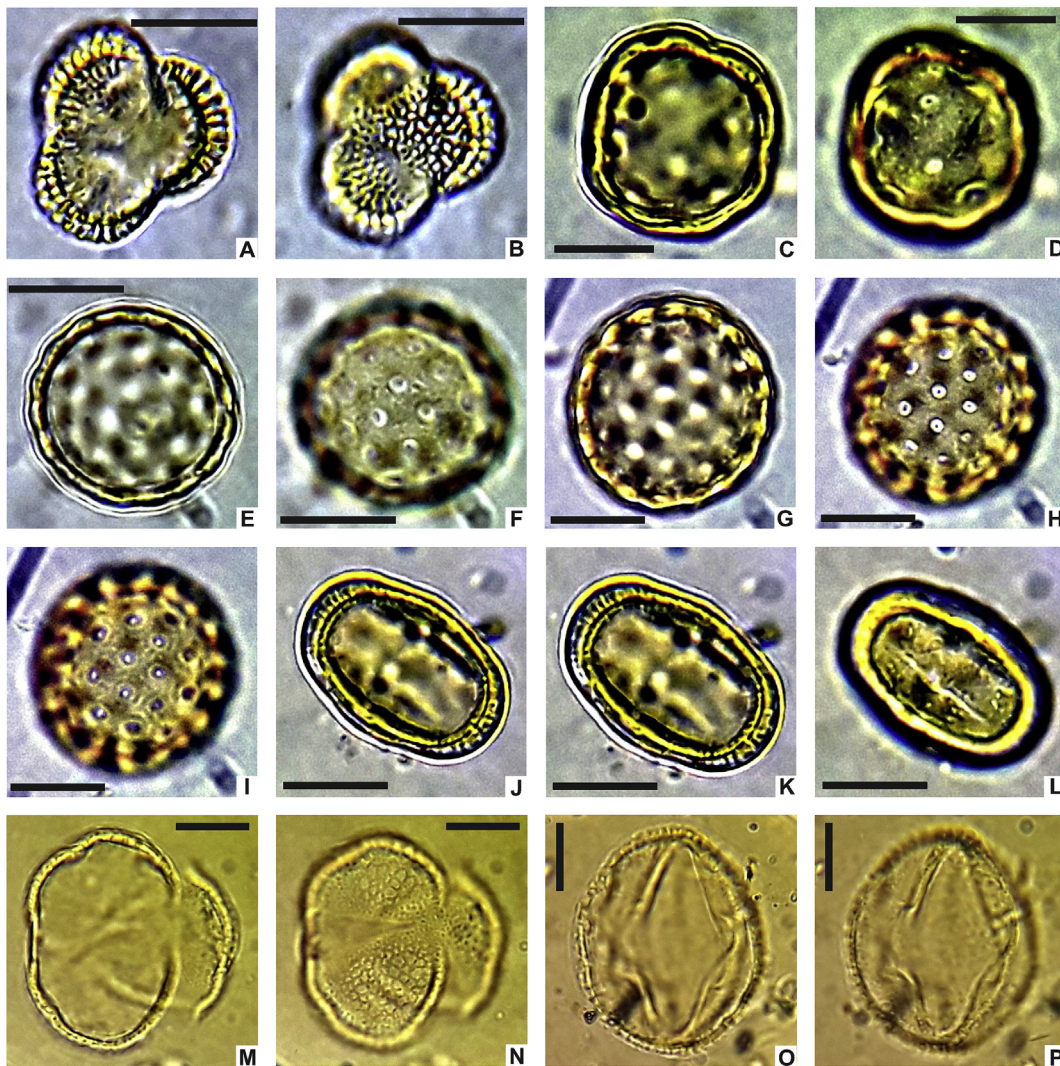**Comparisons:** our specimens agree with the description of *Pohlia*

Plate I. *Rorippa bonariensis*: A-polar view in optical section; B- polar view in superior focus. *Amaranthus muricatus*: C- general view in optical section; D-general view in superior focus. *Chenopodium haumanii*: E − general view in optical section; F- general view in superior focus. *Salicornia ambigua*: G-general view in optical section; H- general view in superior focus; I- general view in superior focus. *Chrysophyllum marginatum*: J-equatorial view in optical section; K- equatorial view in optical section; L-equatorial view in superior focus. *Gleditsia amorphoides*: M-polar view in optical section; N- polar view in superior focus; O- equatorial view in optical section; P- equatorial view in superior focus. *Scale bar = 10 µm.*

wilsonii (Suárez and Schiavone, 2011).

Division CHLOROPHYTA Pascher, 1914
Class CHLOROPHYCEAE Wille, 1884
Order CHLOROCOCCALES Pascher, 1915
Family HYDRODICTYACEAE Dumortier, 1829.
Genus Pediastrum Meyen, 1829
Pediastrum tetras (Ehrenberg) Ralfs, 1845 (Plate II, K).
Description: coenobium circular with eight cells without inter-cellular spaces. Marginal cells divided into two lobes by a deep linear to cuneate incision on the outer side reaching to the middle of the cell; each lobe truncate, slightly emarginated or further divided into two lobes. Inner cells 4–6 sided with a single linear incision. Colonies 29–32 µm in diameter; cells 7–12 µm in diameter.
Main studied material: PMP-CTES. N°: 3613; 3614.
Comparisons: Our specimens agree with the morphology of *Pediastrum tetras*, a well-known cosmopolitan taxon (e.g., Zamaloa and Tell, 2005; Novelo, 2012).

Class TREBOUXIOPHYCEAE Friedl, 1995.
Order TREBOUXIALES Friedl, 1995.
Genus *Botryococcus* Kützing, 1849.
***Botryococcus* sp.** (Plate II, L)

Description: simple colonies of different shapes 41–53 µm, the cells are in small groups at ends of mucilaginous strands, with a yellow sheath and radially arranged 1.7–2 µm thick.
Main studied material: PMP-CTES. N°: 3611.
Kingdom FUNGI Linnaeus, 1753.
Division ASCOMYCOTA Cavalier-Smith, 1998.
Class DOTHIDEOMYCETES Eriksson & Winka, 1997.
Order BOTRYOSPHAERIALES Schoch et al., 2006.
Family BOTRYOSPHAERIACEAETheissen & Sydow, 1918Genus *Dichomera* Cooke, 1878.
***Dichomera* sp.** (Plate II, M)
Description: simple conidia of dark brown color, globose, ovoid or ellipsoid, several-celled with oblique septa; 1 µm thick wall; stockings 12 × 9 µm.
Main studied material: PMP-CTES. N°: 3611; 3616.
Comparisons: *Dichomera eucalypti* (G. Winter), most widespread and important pathogens of woody plants (Barber et al., 2005) is comparable to our specimens.
Order PLEOSPORALES Luttrel ex Barr, 1987.
Family PHAEOSPHAERIACEAE Barr, 1979.
Genus *Phaeoseptoria* Spegazzini, 1908.

Plate II. *Parapiptadenia rigida*: A-general view in superior focus. *Croton urucurana*: B- general view in optical section; C- general view in superior focus; D-general view in superior focus. *Eugenia repanda*: E − equatorial view in optical section; F- equatorial view in optical section; G-equatorial view in superior focus. *Andropogon bicornis*: H- equatorial view in superior focus. *Micrograma squamulosa*: I- equatorial view in superior focus. *Pohlia wilsonii*: J-general view in superior focus. *Pediastrum tetras*: K- general view in superior focus. *Botryococcus* sp.: L-general view in superior focus. *Dichomera* sp.: M-general view in superior focus. *Phaeoseptoria* sp.: N- general view in superior focus. *Phragmotrichum* sp.: O- general view in superior focus. *Agaricus* sp.: P- general view in superior focus. *Scale bar* = 10 μm.

Phaeoseptoria sp. (Plate II, N)

Description: conidia yellow to light brown, elongate to filiform, septate, smooth, truncated base, obtuse apex; hyaline, 6-7 septa, sub-globose to subrectangular cells; 1.5 μm thick wall; measures 15–18 x 3–4.3 μm.

Main studied material: PMP-CTES. Nº: 3612; 3613.

Comparisons: *Phaeoseptoria peltigerae* (Punithalingam and Spooner, 1997), it is similar in shape and size to our specimens but differs in having less septae.

Class INCERTAE SEDIS.
Order INCERTAE SEDIS.
Family INCERTAE SEDIS.
Genus *Phragmotrichum* Kunze, 1823.

Phragmotrichum sp. (Plate II, O)

Description: short conidia, reddish, ellipsoidal, obtuse at apex and truncate at base; septate and constricted in septa; wall 0.8–1 μm thick; measurements 21–30 × 9.2–10 μm.

Main studied material: PMP-CTES. Nº: 3611.

Comparisons: *Phragmotrichum pini* (Cooke) (Sutton and Sandhu, 1969) is morphologically similar to our specimens.

Division BASIDIOMYCOTA Moore, 1980.

Class AGARICOMYCETES Doweld, 2001.
Order AGARICALES Underwood, 1899.
Family AGARICACEAE Chevallier, 1826.
Genus *Agaricus* Linnaeus, 1753.

Agaricus sp. (Plate II, P)

Description: spores not amyloid, honey brown, elliptical; 1.2 μm thick wall; size 8–10 x 5–5.5 μm.

Main studied material: PMP-CTES. Nº: 3614; 3616.

Comparisons: Our specimens are included in *Agaricus* because they share the main features that include smooth, subglobose or ovoid spores of small size 7–11 x 5–6 μm (see Moreno, 1980).

5. Discussion

The qualitative-quantitative composition of the ten assemblages obtained from the carapace of the turtle *Chelonoidis lutzae* and the upper section of lower member of the Toropí/Yupoí Formation indicates that angiosperm pollen grains are more diverse and relatively more abundant than those of fern and fungal and algae (Fig. 3). Major groups of angiosperms include these Brassicaceae (5%–15%), Amaranthaceae (5%–16%), Poaceae (2%–16%), Sapotaceae (5%–13%), Fabaceae

(5%–20%), Euphorbiaceae (2%–15%) and Myrtaceae (5%–10%). The remaining ones are Bryophyta (5%–11%), *Microgramma squamulosa* (5%–15%), *Pediastrum tetras* (2%–15%), *Botryococcus* sp. (5%–10%), and fungal spores Ascomycota type *Dichomera* sp. (2%–12%), *Phaeoseptoria* sp. (2%–13%), *Phragmotrichum* sp. (3%–14%) and Basidiomycota *Agaricus* sp. (1%–11%).

Different ecological requirements of the taxa found in the assemblages support the recognition of two palaeocommunities: a) herbaceous steppe integrated by *Rorippa bonariensis, Amaranthus muricatus, Chenopodium haumanii, Salicornia ambigua, Andropogon bicornis* and vegetative structures of Bryophyta; b) riverbank forest integrated by *Chrysophyllum marginatum* in the shrub stratum; *Gleditsia amorphoides, Parapiptadenia rigida, Croton urucurana* and *Eugenia uniflora* in the arboreal stratum, *Microgramma squamulosa* (epiphyte) and pathogens of woody plants (*Dichomera* sp., *Phaeoseptoria* sp., *Phragmotrichum* sp. and*Agaricus* sp.) Both palaeocommunities are associated with close fresh water bodies indicated by the presence of *Botryococcus* and *Pediastrum tetras* (Fernandez Pacella et al., 2018).

The herbaceous steppe and vegetative structures of Bryophyta suggest periodic desiccation of water bodies that would indicate environmental disturbances probably due to intense wind action under semi-arid conditions (Salazar Allen, 2011; Fernandez Pacella and Lara, 2019; among others). Likewise, the presence of planktonic *Pediastrum tetras*, characteristic of mesotrophic and eutrophic waters of ponds, swamps and shallow lakes (Zamaloa and Tell, 2005), and simple colonies of different shapes of *Botryococcus* sp. indicate an increase in the nutrient load to the basin. One possible mechanism that could explain this greater contribution of nutrients would be the alternation between dry and wet periods. During humid periods, the decomposition of organic material generates being available in soils prevailed whereas erosive processes occurred during dry periods into the basin (Stutz et al., 2014). On the other hand, the riverbank forest would indicate sub-humid climatic conditions, since the genera *Chrysophyllum, Gleditsia, Parapiptadenia, Croton* and *Eugenia* are frequently part of the arboreal strata in riverbank forests associated to courses of rivers and streams under humid conditions (Carnevalli, 1994).

This type of environment agrees with Wagner (1993), who points out that giant turtles are poikilothermic diapsids so they need to live close to water bodies in order to remove the excess of heating from their large bodies. Possibly, this is the strategy used by giant land turtles such as *Chelonoidis lutzae*, which inhabited during the Late Pleistocene in Corrientes province (Zacarías et al., 2013). Hence, the palynological evidence leads us to infer that extinct *Ch. lutzae* would have lived in plains dominated by herbaceous plants close to lakes and ponds and rivers (Fig. 4).

The presence of herbaceous species corroborates the occurrence of herbaceous phytoliths documented in the Toropí/Yupoí Formation in Arroyo Toropí (Erra et al., 2013). On the other hand, the presence of diatoms and spicules of sponges suggest the development of grasslands close to water bodies, in addition to the occurrence of trees or shrubs present in the vegetation (Erra et al., 2013; Contreras et al., 2019).

Therefore, the micro-and megafossils documented have different ecological requirements and support for the Toropí/Yupoí Formation cropping out in the study area (Arroyo Toropí), a dynamic scenario typical of ecotonal zones affected by changes of palaeoclimatic conditions more than other coeval formations (e.g. Tezanos Pinto, Lomita del Indio and Carcarañá Formations) of the Chaco-Pampa plain (Iriondo, 2010). The paleofaunas and palynological data confirm the predominance of a climate with arid/semi-arid lapses and other warm/humid with the development of open/semi-open environments dominated by grasses and trees or shrubs close to lentic water bodies. Hence, a different climate prevailed in the Mesopotamian region whereas relatively cold and arid conditions occurred in the Pampean region during the Pleistocene (Tonni et al., 1999). Additionally, high concentrations of montmorillonites, illites and kaolinites (clays) reinforce the interpretation of well-marked seasons characterized by semi-arid and humid- and temperate phases (Iriondo, 2007). These variable climatic conditions are in the geo-climatic context of MIS 3 El Niño and Niña (ENSO) phenomena. Meerbeeck et al. (2009) postulate that climatic conditions of MIS 3 with respect to the Last Glacial Maximum [LGM, MIS 2] were 2 °C warmer registering alternations of cold periods of 1.7 °C MIS 3-sta (stadial) and warm 2.0 °C MIS3 (interstadial). In contrast, Martínez (2009) proposed that during Mid-Late Pleistocene transition, there was a change between conditions of El Niño (humid climate with higher rainfall) to La Niña (more arid climate with low rainfall). During the Last Maximum Glacial in the Mesopotamian region, more complex conditions occurred with predominance of Niña-type climate with less occurrences of El Niño phenomenon (Zacarías et al., 2014).

6. Conclusion

The palynologic study carried out in samples obtained from the carapace of the turtle *Chelonoidis lutzae* and sediments present in the Toropí/Yupoí Formation (Arroyo Toropí, Bella Vista) contributed to a better understanding of its palaeoclimatic and palaeoenvironmental interpretation.

The quali-quantitative information of terrestrial and aquatic groups of palynomorphs documented in the association indicate the development of dynamic scenarios typical of ecotonal zones. Herbaceous palaeocommunities associated to arboreal or shrubby elements (*Chrysophyllum, Gleditsia, Parapiptadenia, Croton* and *Eugenia*) close to fresh waters bodies developed under arid/semi-arid and warm and more humid seasonal climate. This result is in agreement with previous studies on faunas and phytolith and clay minerals of the Mesopotamian region during the late Pleistocene.

CRediT authorship contribution statement

L. Fernandez Pacella: Conceptualization, Methodology, Formal analysis, Investigation, Resources, Data curation. **G.G. Zacarías:** Conceptualization, Writing - review & editing. **M. Di Pasquo:** Writing - review & editing.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jsames.2019.102476.

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