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Palinología del Meso-Cenozoico de Argentina

Volumen en homenaje a Mirta Elena Quattrocchio

Marcelo A. Martínez y Daniela E. Olivera, Editores.
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PALINOLOGÍA DEL MESO-CENOZOICO DE ARGENTINA

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2016

PRÓLOGO

"Enseñar es dejar una huella en las vidas....... para siempre"

Dra. Mirta Elena Quattrocchio

Este volumen está dedicado a la Dra. Mirta Elena Quattrocchio, una de las investigadoras más destacadas en el campo de la Palinología a nivel nacional e internacional.

Hemos escogido como portada una imagen panorámica del formidable cañón del Picún Leufú, en la provincia del Neuquén, dado que el ámbito de la Cuenca Neuquina ha sido motivo de gran parte de la producción científica de Mirta, de la mano de su formador el Dr. Wolfgang Volkheimer y luego acompañada por varios de sus discípulos. Al igual que este pequeño curso de agua fue labrando en el paisaje una huella imborrable durante miles de años, la labor fecunda de Mirta desde la docencia, con su mirada sobre la ciencia y la investigación, marcaron para siempre la vida profesional de quienes hemos aprendido y aún lo seguimos haciendo a su lado, multiplicando, tal vez sin tener conciencia de la real magnitud, su influencia y legado en varias generaciones de investigadores y docentes.

En 1972, Mirta obtiene el título de Licenciada en Ciencias Geológicas en la Universidad Nacional del Sur (UNS, Bahía Blanca). Siendo muy joven aún, ingresa en la docencia universitaria y se desempeña por más de 40 años en todas las categorías docentes ordinarias en asignaturas de grado, cursos, seminarios de posgrado y conferencias. Recientemente ha sido reconocida como Profesora Extraordinaria (Consulta) del Departamento de Geología de la UNS. Su campo de actuación no solo se limita a la UNS, sino también a otros centros educativo/científicos de prestigio nacional, como el Instituto Universitario de Trelew, la Universidad Nacional de La Pampa y la Facultad de Ciencias Exactas y Naturales y Agrimensura de Corrientes e internacional, como el Instituto Smithsonian de Investigaciones Tropicales de Panamá, el Centro de Investigaciones Científicas y de Educación Superior de Ensenada de México, la Universidad Internacional de Andalucía, la Universidad Federal de Rio Grande Do Sul y la Universidade do Valle do Rio dos Santos de Brasil.

"Hay hombres que luchan un día y son buenos.
Hay otros que luchan un año y son mejores.
Hay quienes luchan muchos años, y son muy buenos.
Pero hay los que luchan toda la vida, esos
son los imprescindibles"

Bertolt Brecht

En 1972 inició sus primeros pasos en la investigación palinológica junto a su primer maestro el Dr. Wolfgang Volkheimer, alcanzando en 1977 el título de Dra. en Geología. Desde entonces, y de manera incansable y sostenida, abocó todos sus esfuerzos al desarrollo de la Palinología como disciplina bioestratigráfica. Tras más de 40 años de gestión logró conformar un fuerte grupo de trabajo y constituyó el Laboratorio de Palinología de la UNS, uno de los más importantes y numeroso del país con proyección internacional. Sus investigaciones fueron pioneras en distintas áreas y temáticas. En este sentido el Análisis Palinofacial como herramienta para interpretar condiciones paleoambientales y potencial oleogenético por ella impulsado continúa siendo una temática que es llevada a cabo en pocas instituciones palinológicas del país.

Este volumen consta de ocho contribuciones, cuyas autorías corresponden a algunos de los que fuimos orientados por la Dra. Mirta Quattrocchio, durante distintas etapas de su carrera. La versatilidad y habilidad de Mirta para conformar grupos de trabajo heterogéneos, así como su visión holística de las ciencias se evidencian en la multidisciplinariedad de temáticas abordadas en este volumen. Ya sea bajo la figura de becarios, docentes, integrantes de proyectos, técnicos, investigadores o personal de apoyo, todos quienes hemos tenido la fortuna de interactuar con Mirta de alguna u otra manera, reconocemos en ella a un ser humano de características extraordinarias con una gran generosidad, siempre atenta a las necesidades y problemáticas del prójimo.

Cuadro del Golfo de Panamá, visto desde la Isla Taboga en el Pacífico, pintado por Mirta, otra de sus pasiones.

Las contribuciones incluidas en este volumen han sido distribuidas siguiendo un criterio estratigráfico y regional. En la primera parte se incluyen tres artículos en depósitos mesozoicos, uno en la provincia de Chubut y dos en la Cuenca Neuquina. En la segunda parte se incluyen cuatro trabajos realizados en depósitos del Cenozoico, dos en la provincia de Buenos Aires y dos en Tierra del Fuego. La contribución invitada sintetiza y actualiza la biocronoestratigrafía de la provincia de Buenos Aires a partir del registro de vertebrados. Este trabajo es de autoría de colaboradores muy cercanos a los afectos de Mirta Quattrocchio, por lo que hemos considerado valiosa su inclusión.

Queremos expresar un profundo agradecimiento a los autores, a los árbitros de cada uno de los artículos de este volumen, al equipo de producción editorial y gráfica de PE-APA y a los directores de la Publicación Electrónica de la Asociación Paleontológica Argentina, M. Susana Bargo e Ignacio H. Escapa por brindar lo mejor de sí y transformarse en facilitadores de este humilde homenaje.

Marcelo A. Martínez y Daniela E. Olivera

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ANCIENT COASTAL ENVIRONMENTS IN A MAASTRICHTIAN–?PALEOCENE ATLANTIC SHORELINE: A PHYTOPLANKTON APPROACH

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Abstract. In this contribution we describe planktonic assemblages, comprising their taxonomic composition and palaeoecological attributes, from the La Colonia Formation, Patagonia, Argentina. The palynological samples are from the section exposed at Estancia San Miguel, in the Telsen area, Chubut province. Diverse organic-walled remains of Chlorophyta and Charophyta taxa are documented. These include coenobia of two species of *Pseudopediastrum*, colonies of *Botryococcus* and zygospores of the form-genus *Ovoidites* (resembling extant genera of Zygnemataceae). The green algae together with dinoflagellate cysts (analyzed in a previous detailed study) indicate brackish to freshwater and freshwater depositional conditions for the middle and upper part of the Estancia San Miguel section, respectively. These water bodies developed along a coastal plain in the northern Patagonia probably during the Paleocene, in a phase of the extensive first transgressive event of the South Atlantic. The earliest record of *Pseudopediastrum brevicorne* for Patagonia is presented.

Key words. Organic-walled algae. Palaeoecology. Fresh/brackish water. Maastrichtian–?Paleocene. Patagonia.

Resumen. ANTIGUOS AMBIENTES COSTEROS EN UNA LÍNEA DE COSTA ATLÁNTICA DEL MAASTRICHTIANO–?PALEOCENO: UN ENFOQUE DESDE EL FITOPLANCTON. En esta contribución se presentan asociaciones planctónicas, incluyendo sus aspectos taxonómicos y atributos paleoecológicos, de la Formación La Colonia, Patagonia, Argentina. Las muestras palinológicas estudiadas provienen de la sección expuesta en Estancia San Miguel, área de Telsen, provincia de Chubut. Se documentan diversos elementos de pared orgánica de taxones de Chlorophyta y Charophyta. Estos incluyen cenobios de dos especies de *Pseudopediastrum*, colonias de *Botryococcus* y cigósporas del morfogénero *Ovoidites* (similares a cigósporas de géneros actuales de Zygnemataceae). Las algas verdes junto a los quistes de dinoflagelados (presentados en un detallado estudio previo) indican condiciones depositacionales de agua salobre a dulce para la parte media y de agua dulce para la parte superior de la sección Estancia San Miguel. Estos cuerpos de agua se desarrollaron a lo largo de una planicie costera en el norte de Patagonia, posiblemente durante el Paleoceno, en una fase del extenso primer evento transgresivo del Atlántico Sud. Se presenta el registro más temprano de *Pseudopediastrum brevicorne* para Patagonia.

Palabras clave. Algas de pared orgánica. Paleoecología. Agua dulce/salobre. Maastrichtiano–?Paleoceno. Patagonia.

DURING the Late Cretaceous–early Paleocene, the southern region of South America was characterized by relatively calm tectonic conditions and subjected to an overall transgressive phase of deposition (Uliana and Biddle, 1988). Wide areas of the extra Andean Patagonia were covered by the sea during the first Atlantic transgression recognized in the region (Gasparini *et al*., 2015). The maximum extension of the coastline toward the continent occurred during the Maastrichtian, extending the marine influence up to the foot of the Andes (Malumián and Nañez, 2011). This transgression allowed developing an epicontinental sea that gave rise to various marginal marine and shallow marine shelf environments, because it did not achieve great depth (Nañez and Malumián, 2008). As a consequence, a series of Late Cretaceous coastal plain sedimentary deposits accumulated, which represent estuaries, deltas, and lagoon/barrier complexes (Spalletti, 1996; Franzese *et al.*, 2003; Scasso *et al.*, 2012). In the area of the Somuncurá Plateau, northern Patagonia, these deposits correspond to the Allen, Coli Toro, Los Alamitos, Paso del Sapo, Lefipán and La Colonia formations (Page *et al.*, 1999).

In particular, the La Colonia Formation is widely exposed along the southeastern margin of the Somuncurá Plateau in Chubut Province, and has been extensively studied from stratigraphic, sedimentological and palaeontological approaches. Continental and marine fossils are indicative of the coastal nature of the depositional environments for the La Colonia Formation (Gasparini *et al.*, 2015 and references therein). Low diversity foraminifera assemblages from the Maastrichtian beds at Bajada Moreno (Northern Patagonia), included within the La Colonia Formation, also reflect marginal shallow marine settings (Nañez and Malumián, 2008).

Studies of the megaflora and palynological records from the La Colonia Formation have been previously published by Archangelsky *et al.* (1999), Archangelsky and Zamaloa (2003), Gandolfo and Cúneo (2005), Cúneo *et al.* (2013, 2014) and Gandolfo *et al.* (2014). Recently, the palynological composition of the La Colonia Formation exposed at the Estancia San Miguel section, in the area of Telsen, Chubut, was analyzed with emphasis on the description of neritic marine and fresh- to brackish water dinoflagellate cysts (Guler *et al.*, 2014). In that work we also showed the high frequencies reached by the green microalgae, and their palaeoecological significance for the environmental interpretation of these deposits. Notably, records of the freshwater to brackish microalgae are not abundant for the Late Cretaceous–Paleocene of Patagonia, even though widespread favorable habitats are identified by the lithofacies associations. The occurrence of species of *Pediastrum*, *Botryococcus* and of Zygnemataceae spores have been recognized in two plant bearing sections of the La Colonia Formation at the Cerro Bosta and Cañadón del Irupé/Quebrada del Helecho localities (Cúneo *et al.*, 2014). From the nearby Paleocene (Danian)-aged Bororó Formation, Scafati *et al.* (2009) recorded *Botryococcu*s, *Coelastrum* and also Zygnemataceae spores in lacustrine beds. Likewise, Prámparo *et al.* (2006, 2008) interpreted lacustrine environment in a Late Cretaceous sauropod track site at Agua del Choique (southern Mendoza province, western Argentina) in the upper part of the Loncoche Formation, mainly based on the microalgae content. In that locality, the palynological associations are dominated by species of *Pediastrum* accompanied by representatives of *Botryococcus*, peridinioid dinoflagellate cysts and a few specimens of *Ovoidite*s and *Tetraporina*.

The main objective of this contribution is to document the organic-walled green algae and other aquatic palynomorphs that integrate the planktonic assemblages from the La Colonia Formation exposed at the Estancia San Miguel section together with dinoflagellate cysts previously described in Guler *et al.* (2014). Although this contribution is not intended to be an exhaustive taxonomic analysis, diagnostic characteristics of the studied planktonic remains are considered. We also summarize the ecological interpretation of these brackish to freshwater Maastrichtian–?Paleocene microalgae and other palynobiota assemblages. They constitute a significant tool for making palaeoenvironmental interpretations in the ancient marine marginal setting of the Patagonian region.

GEOLOGICAL AND SEDIMENTOLOGICAL SETTING

The palynological samples analyzed herein were obtained from exposures of the La Colonia Formation in the Telsen area, northeast of the Somuncurá-Cañadón Asfalto Basin, Chubut Province (Fig. 1). In this area, volcanic rocks of the Marifil Formation (182 My–185 My, Navarro *et al.*, 2015) constitute the basement. The La Colonia Formation overlies in sharp contact the fluvial deposits of the Albian Chubut Group (109 My, Navarro *et al.*, 2015), which are the oldest sedimentary rocks in Telsen. The thickness of the La Colonia Formation does not exceed 25 m in the Telsen area, but is thicker (up to approximately 205 m thick) in the center and west of the Somuncurá-Cañadón Asfalto Basin (Navarro, 2012). This is a result of a regional unconformity revealed by a progressive wedging from the south to the north, up to disappearance of these strata in the area of Cañadón Williams (Fig. 1) (Navarro *et al.*, 2015). The La Colonia beds are overlain by the Oligocene volcanics of the Somun Curá Formation (26 My, Ardolino and Franchi, 1996).

The sedimentology of the La Colonia Formation in the

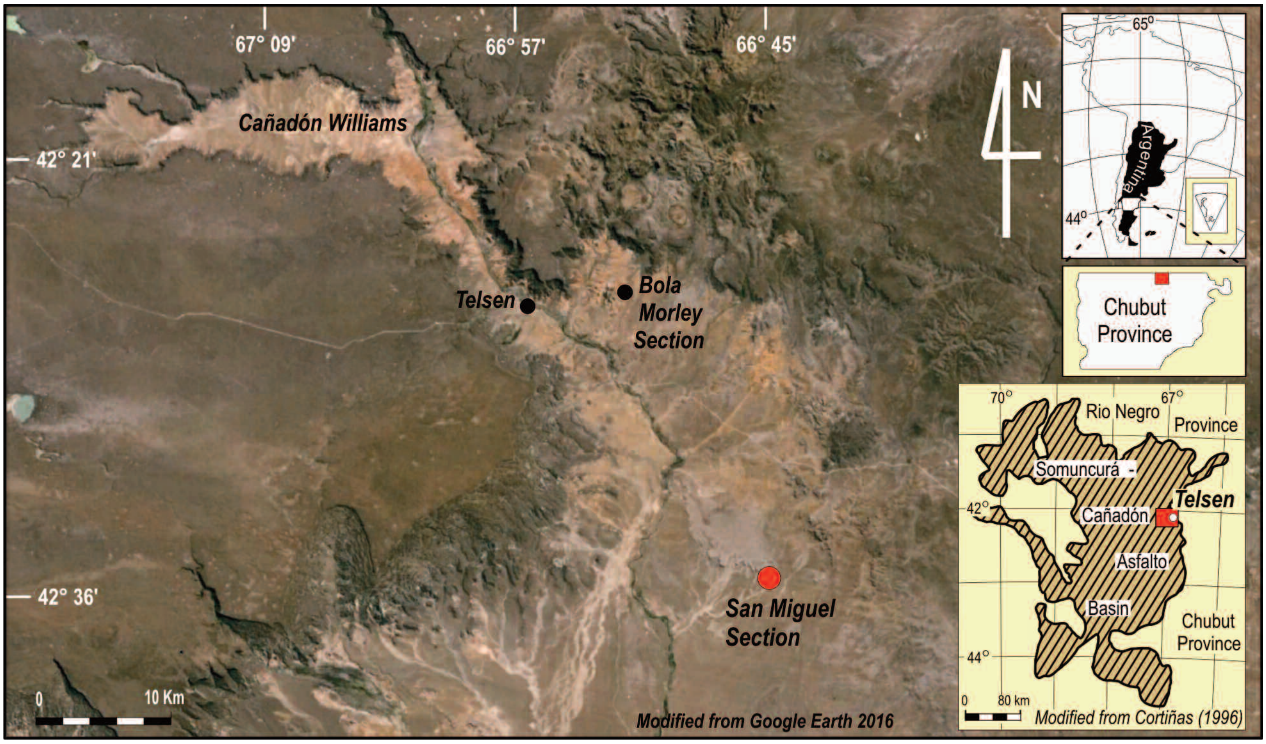


Figure 1. Location map of the Telsen area, Chubut Province, Argentina.

Telsen area is based on data collected from three sites (Fig. 1). The lower part of the unit was described in the vicinity of Telsen and the Bola Morley Hills (Navarro, 2012), where a basal lag of veneer conglomerate overlies a ravinement erosion surface. The latter, represents a key surface in a sequence stratigraphic context, given alternatively by wave or tidal energy, rapidly retreating coast lines and locates at the base of transgressive or high-stand systems tracts (*cf*. Posamentier and Allen, 1999; Chaumillon *et al*., 2010). Above the basal conglomerate, four facies associations were recognized: a) shoreface to off-shore transition, b) tidal flats, c) lagoons with tidal influence, and d) ponds and shallow lakes without marine influence (Navarro, 2012; Navarro *et al*., 2012). The two first facies associations were also recognized in the vicinity of Telsen and the Bola Morley Hills (Fig. 1). The 14.5 meter-thick Estancia San Miguel section, where intertidal and lacustrine facies with and without marine connection are represented, is shown in Figure 2. Facies associations recognized throughout the San Miguel section show two well-defined intervals characterizing a lower storm-dominated shoreface to offshore transition, and an upper tidal flat to lacustrine zone reflecting an overall coastline progradation during a high-stand stage. The lower section is predominantly composed of fine-grained thin- medium-bedded laminated sandstones with convolute structures overlying a strongly bioturbated siltstone interval. Hummocky and swaley cross-stratification within the laminated sandstones, indicate high-energy wave-induced bed forms related to storm episodes (Navarro *et al.,* 2012). The upper intertidal-flat facies association contains thoroughly developed heterolithic facies (flaser, lenticular and wavy lamination) associated within subtle coarsening upward cycles. Mudstones within this association show pervasive bioturbation; however, little bioturbated intervals show muddy rhythmites and intraclastic mud-chip conglomerates representing upper intertidal flats with intermittent exposure (Navarro *et al.,* 2012). The uppermost part of the section, in apparent continuity, is represented by ~4 m of a massive bioturbated slightly muddy more greenish to yellowish section without sandy laminae.

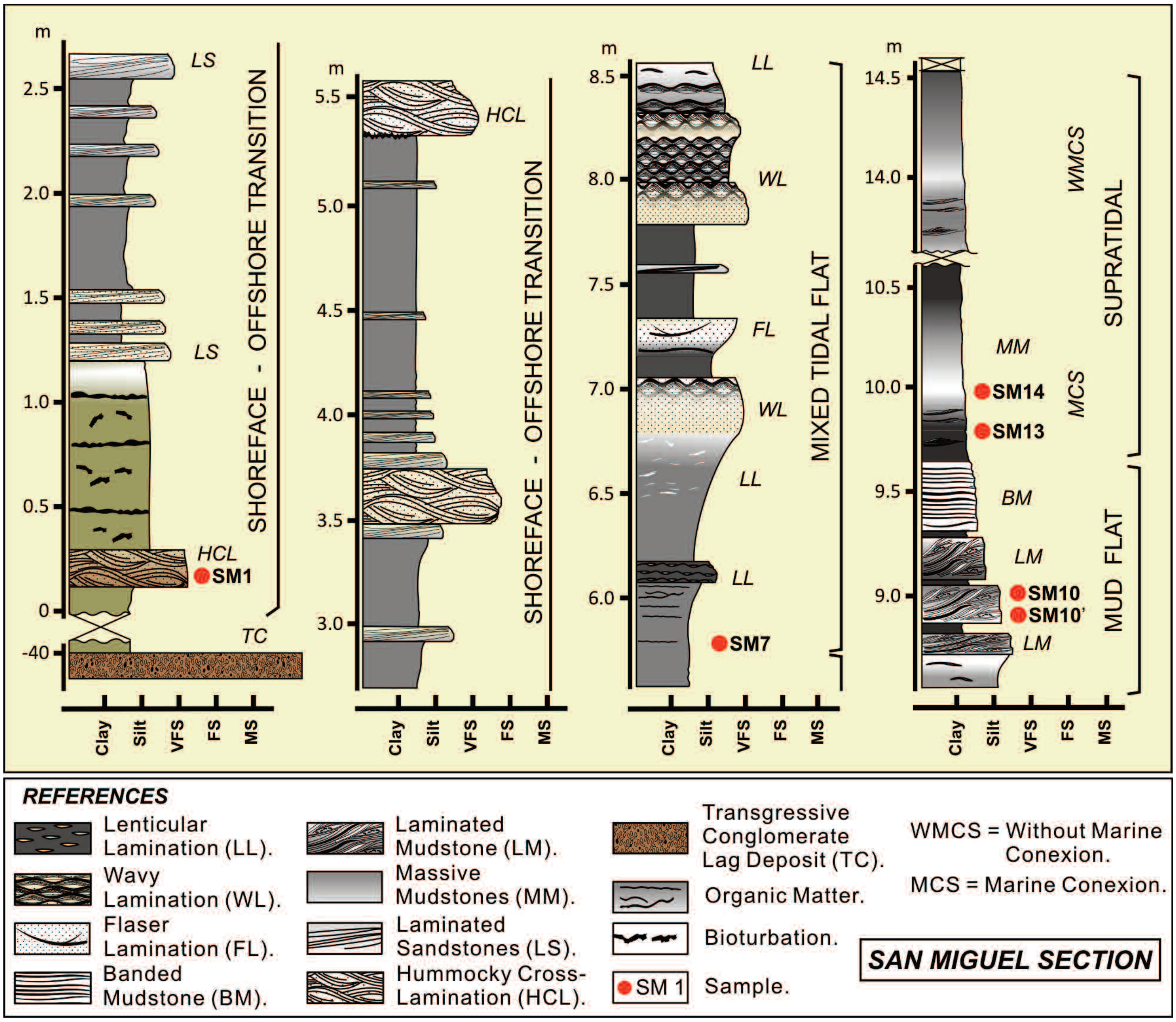


Figure 2. Stratigraphic section of the La Colonia Formation at the Estancia San Miguel locality, showing the distribution of facies and productive palynological samples.

AGE

The deposits at the Estancia San Miguel section represent the uppermost part of the La Colonia Formation in the Telsen Area (Navarro *et al.*, 2012). Based on micropalaeontological data, foraminifera and ostracods, a Campanian/Maastrichtian age was indicated for the upper marine deposits of the unit (Ardolino and Franchi, 1996 and references cited therein). A Maastrichtian age was established by Náñez and Malumián (2008) who studied the foraminiferal assemblages of the marine layers of the La Colonia Formation at the Bajada Moreno section, 100 km south of Telsen. Palynological data together with a stratigraphical criterion suggested an age not older that Paleocene for the uppermost part of the unit in the Telsen area, even though the age of the marine part of the La Colonia Formation is probably Late Cretaceous–early Paleogene (Guler *et al.*, 2014).

MATERIAL AND METHODS

Samples were collected at a regular distance of 20–30 cm from the base to the top of the Estancia San Miguel section where the La Colonia Formation outcropped. Following standard techniques, the palynological processing of the samples included HCl and HF for removal of carbonates and silicates, respectively. Organic residues were sieved at 10 and 20 µm, stained with Bismarck C and mounted in glycerine jelly. Light microscopy observation of the slides was at 600× and 1000× magnification using a Nikon Eclipse 600 (serial number 77255). For the quantitative analysis, more than 300 palynomorphs (including dinoflagellate cysts, algae, spores and pollen grains) were counted in the palynological-fertile levels, except for sample SM7 in which the palynomorph number was <300 after examining the entire organic residue. The frequencies were calculated over the sum of total palynomorphs.

The classification of the Chlorophyta and Charophyta used in the text follows that of Lewis and McCourt (2004). For the dinoflagellate cysts the classification of Fensome *et al*. (1993) is followed. Images were taken with a Nikon Coolpix 950 digital camera. The microscope coordinates reference follows the sample and slide number for each specimen illustrated. Slides containing the illustrated specimens are stored in the Colección Palinológica, Laboratorio de Palinología (INGEOSUR-UNS), Bahía Blanca, Argentina.

RESULTS

Planktonic algae and invertebrates

Planktonic green microalgae were present in the six palynologically productive samples of the Estancia San Miguel section. The components recognized in the samples contain both reproductive (resting spores) and vegetative stages (coenobia and colonies) belonging to the Chlorophyta and Charophyta algae. The most representative green microalgae, in terms of relative frequencies from the La Colonia Formation in the San Miguel section, were analysed and illustrated in this work. All algal palynomorphs recognised in the samples were placed in each one of the outlined categories in Figure 3. Dinoflagellate cysts (Dinoflagellata) are also an important component of the assemblages and

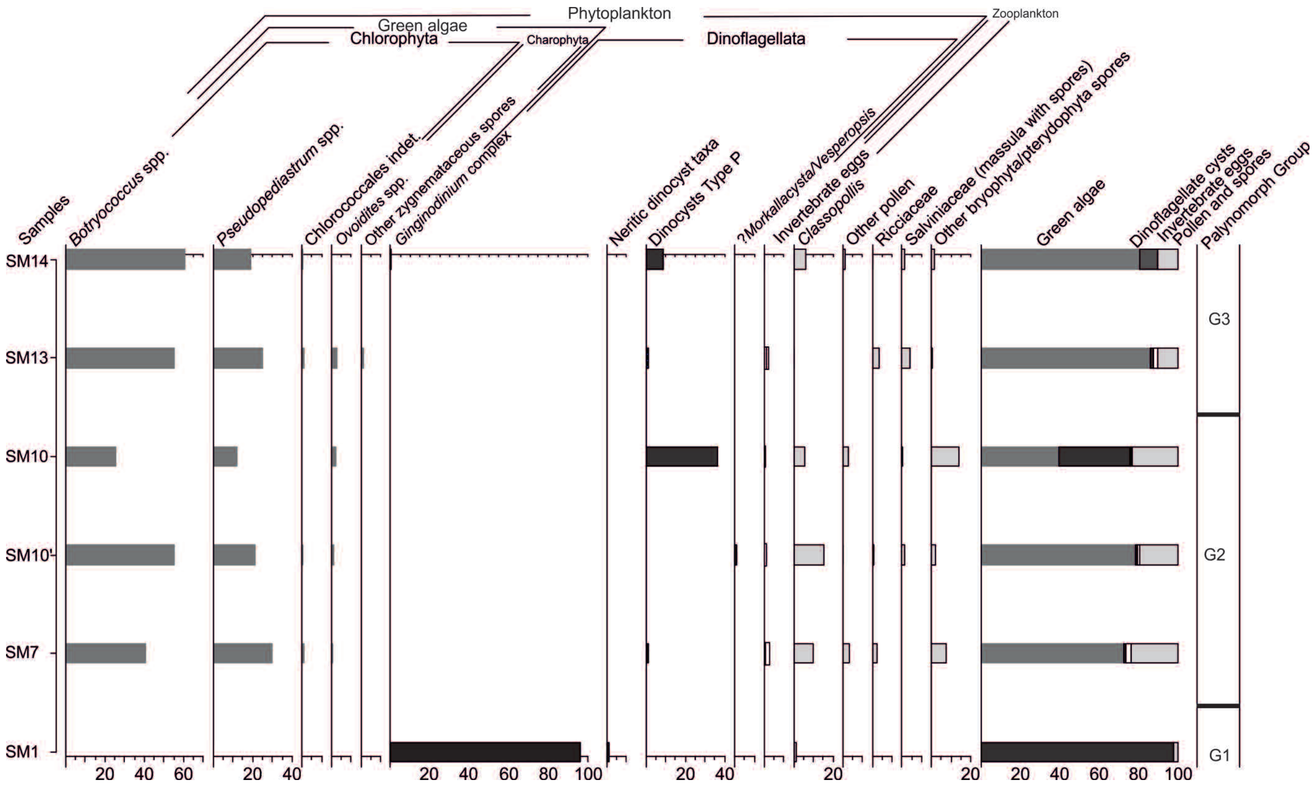


Figure 3. Percentage diagram of algal micro-remains including all palynological components of the samples (modified from Guler *et al.*, 2014) from the La Colonia Formation at San Miguel section.

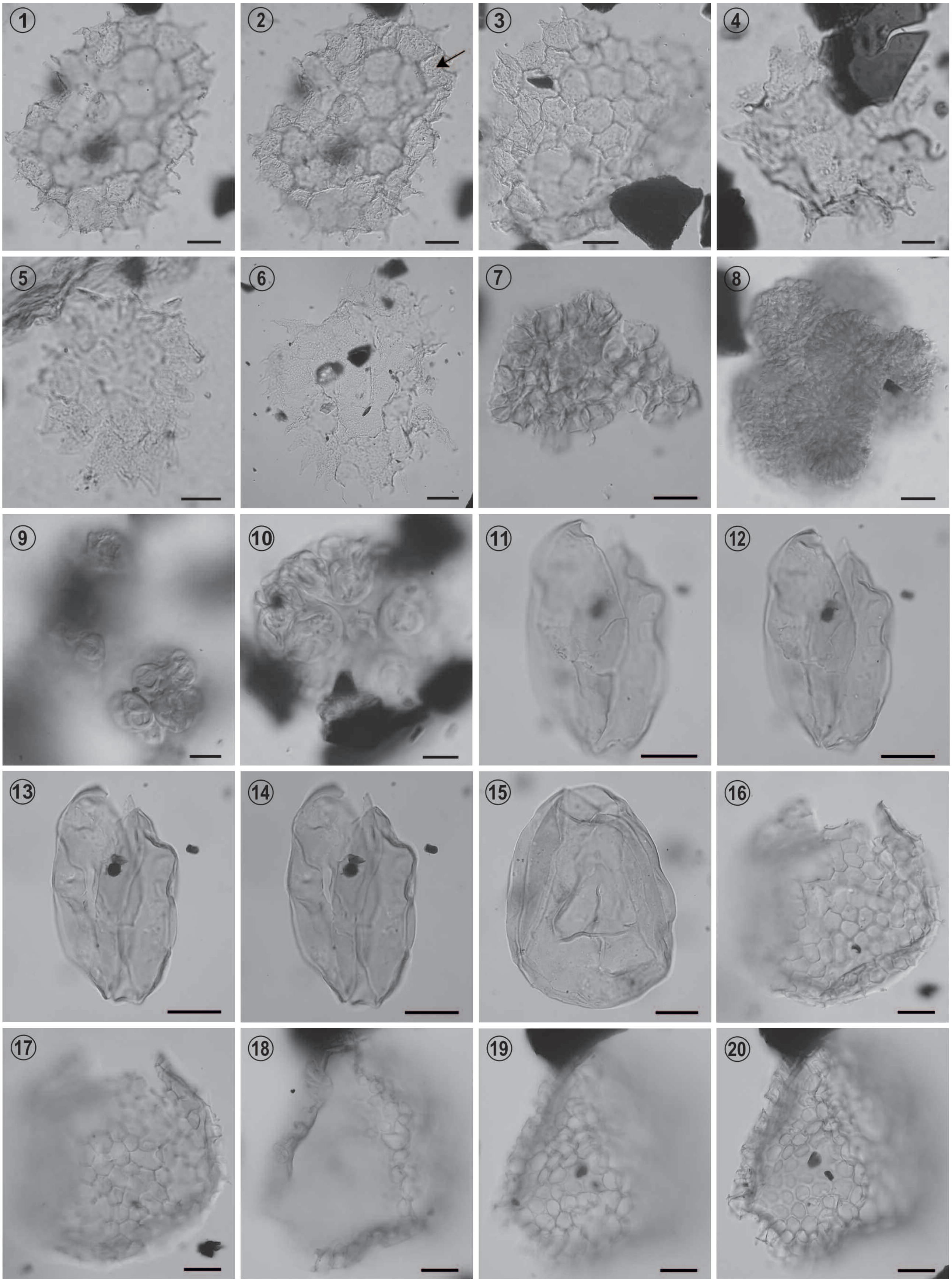
a complete taxonomic discussion of the species is included in Guler *et al*. (2014). Other aquatic palynomorphs identified represent zooplanktonic invertebrate eggs (see List of identified planktonic taxa).

Chlorophyceae. The freshwater Hydrodictyaceae family is well represented in the La Colonia Formation microalgae by different coenobia of the *Pediastrum* group. Recent molecular phylogenetic studies within the Hydrodictyaceae demonstrated that morphologically similar taxa have genetic diversity, and the genus *Pediastrum* Meyen 1829 was split into six genera: *Stauridinium* (Printz) Hegewald 2005, *Monactinus* (Turpin) Hegewald 2005, *Pediastrum, Parapediastrum* Hegewald 2005, *Pseudopediastrum* Hegewald 2005 and *Lacunastrum* McManus 2011 (Buchheim *et al*, 2005; McManus and Lewis, 2005, 2011; McManus *et al*., 2011). According to the present state of knowledge, some coenobia herein recovered can be referred to the extant *Pseudopediastrum brevicorne* (Braun) Jena and Bock 2014, and *Pseudopediastrum boryanum* var. *boryanum* (Turpin) Hegewald 2005 is also identified (Fig. 4.1–5). Other atypical or poorly preserved coenobia cannot be classified without doubt (Fig. 4–6). All morphotypes observed in the samples share morphological similarities, such as granulate cell wall and lack of intercellular spaces. Well-preserved specimens of *Pseudopediastrum brevicorne* exhibit a reticulate wall with conspicuous granules at the junctions of the muri (Fig. 4.2).

In Argentina, living *Pseudopediastrum brevicorne* it is restricted to low latitudes (between *ca*. 28 and 39° S) and its fossil presence at higher latitudes is remarkable (Zamaloa and Tell, 2005). *Pseudopediastrum brevicorne* (as *Pediastrum boryanum* var. *brevicorne*) appeared at higher southern latitudes of Patagonia in the Miocene Pinturas Formation and Cullen Formation (*ca*. 46 and 52° S respectively) and was interpreted as an indicator of mild climate (Zamaloa and Tell, 2005). The occurrence of this species in the phytoplankton of the La Colonia beds is the first published record of this species in the Cretaceous–Paleocene of Argentina and its earliest record. In the Cretaceous–Paleocene record of Argentina only *Pseudopediastrum boryanum* var. *boryanum* (as *Pediastrum boryanum* var. *boryanum*) has been previously recorded (Zamaloa and Tell, 2005). The specimens reported as *Pediastrum* spp. by Cúneo *et al.* (2014) from the La Colonia Formation at Cerro Bosta and Cañadón del Irupé/Quebrada del Helecho sites, could be also allocated (from the illustrations) as *Pseudopediastrum boryanum* var. *boryanum.* Currently *Pseudopediastrum boryanum* var. *boryanum* is widely distributed in Argentina (Tell, 2004) and occurs in a more or less wide range of mesotrophic to eutrophic waters (Komárek and Jankowská, 2001).

Trebouxiophyceae. Remains of colonies of the green fresh- to brackish-water alga *Botryococcus* Kützing 1849 are important components of the palynomorph assemblages of the San Miguel section (Fig. 3). These remains are variable in the shape, size and pattern of radially arranged cups distinguishing different morphological types (Fig. 4.7–10). In living colonies of *Botryococcus*, the individual cells are embedded in an extracellular matrix of polymerized, liquid hydrocarbons that allow colonies to float, presumably to increase exposure to light for photosynthesis at the surfaces of ponds or lakes. Only a few of the required morphologic features evaluated by Komárek and Marvan (1992) to discriminate species of living *Botryococcus* are consistently preserved and available in the fossil material. Additionally, the intraspecific taxonomy is remarkably less well known than in the *Pediastrum*-group, and there are several species

Figure 4. Green algae and invertebrate eggs recovered from the La Colonia Formation at the middle and upper part of the San Miguel section. **1–3,** ***Pseudopediastrum brevicorne*** (Braun) Jena and Bock, **1–2,** SM10′ A 47.5/115.2, **1,** high focus; **2,** intermediate focus, showing a reticulate sculpture; **3,** SM10′ A 42/104.5, general view. **4–5,** ***Pseudopediastrum boryanum* var. *boryanum*** (Turpin) Hegewald, **4,** SM10′ A 58/112.6; **5,** SM10′ A 57.2/122.5. **6,** ***Pseudopediastrum* sp.** SM14/08 B 30.5/96. **7–10,** ***Botryococcus* spp., 7,** SM13/08 D 31.3/119.7, colony with thin walled cups; **8,** SM10′ A 55.5/112, large colony composed of agglomerated subcolonies; **9–10,** circular colonies with thick walled cups arranged in groups of four, **9,** colony composed of small group of connected cells, SM14/08 B 34/106, **10,** SM14/08 B 38.7/115.5. **11–14,** ***Ovoidites parvus*** (Cookson and Detmann) Nakoman, SM13/08 A 40.1/111; high to low focus; **15,** ***Ovoidites grandis*** (Pocock) Zippi, SM13/08 B 51.6/96.5. **16–20,** ***Hexarthra mira*** Hudson, **16–17,** SM13/08 D 35.5/119.4; complete specimen, **16,** high focus, **17,** intermediate focus; **18–20,** SM13/08 B 33.4/104.4, a single half; **18,** high focus; **19,** intermediate focus, **20,** low focus. **1–3, 8, 11–20:** scale bar= 20 µm; **4–7, 9–10:** scale bar= 10 µm.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of uncertain taxonomy (Jankowská and Komárek, 2000; Senousy *et al*., 2004). Given these limitations, in our study the different form-types of *Botryococcus* are not assigned to species. Significantly, the colony form-types reported herein can be compared with the discriminated form-species using SEM analysis *(Botryococcus* sp. 1 to *Botryococcus* sp. 4) from the Danian Bororó Formation, approximately 100 km south from the deposits studied herein (Scafati *et al*., 2009, fig. 5, A–D).

Botryococcus generally lives in freshwater, but considerable abundances in brackish habitats are also known (Batten and Grenfell, 1996). Zippi (1998) refers that it commonly forms water-blooms in alkaline lakes and ponds. At present *Botryococcus* is broadly distributed in tropical to temperate areas (Batten and Grenfell, 1996) and usually abundant in shallow-water pools in case of little precipitation (Guy-Ohlson, 1992). These algae have an oligotrophic to mesotrophic character (Komárek and Marvan, 1992; Chmura *et al*., 2006), however also are reported from eutrophic environments.

Zygnemataceae. Different types of spores of zygnematacean algae are present in small frequencies (up to 5% in sample SM13) in the palynological spectra from La Colonia beds. Most of our specimens are ellipsoidal in equatorial view, with psilate to scabrate wall and composed of two halves with a longitudinal dehiscence (Fig. 4.11–15). The form-genus *Ovoidites* (Potonié) Krutzsch 1959 represents morphotypes identical to zygospores of several species of the extant *Spirogyra* Link 1820 and the related genus *Sirogonium* Kützing 1843 (Van Geel and Grenfell, 1996; Zippi, 1998).

These filamentous green algae are presently widespread in freshwater habitats as slow-moving water, or shallow stagnant ponds (Randhawa, 1959). Generally occurring as free-floating masses, but few members are found attached to substrate in the littoral zone of lakes and in flowing water (Lee, 2008). Species of *Spirogyra* are important primary producers in many aquatic food webs, especially in habitats with neutral or slightly acidic pH values, and the zygospores formation occurs during or toward the end of spring or summer (Gerrath, 2003; Stancheva *et al*., 2013).

Peridiniaceae. Throughout the San Miguel section, rounded-pentagonal peridinioid-shaped, non-pigmented (phototrophic) peridiniacean cysts reach high percentage values (Fig. 3). An almost monotypic assemblage of small, spiny, thin-walled palaeoperidinioid dinoflagellate cysts grouped in ?*Ginginodinium* sp. with significant morphological variability characterizes the base of the section. Although many specimens were observed, in a very few ones it was possible to identify the typical palaeoperidinioid archeopyle; it involves three intercalary and the three dorsal precingular plates (Guler *et al*., 2014: fig. 4.2). Palaeoperidinioid dinoflagellate cysts have been recorded in marine strata since the Cretaceous, however, occurrences in non-marine environments could have occurred since the Cenozoic (Fensome *et al*., 1993).

Dinocysts type P from the middle and upper part of the section, include small translucent extremely thin-walled peridiniacean cysts with a weakly granulate surface and incipient development of one apical and two symmetrical short antapical horns. Most of the specimens occur poorly preserved, most of them folded and, in the few cases where the archeopyle was observed, it was not possible to determine the number or the plate series involved. Apparently, the archeopyle is formed by the loss of precingular, intercalary and/or apical plates, but it could not be accurately defined. Dinocysts type P resemble specimens of *Saeptodinium* Harris 1974 from Australian non-marine Paleocene deposits (Harris, 1974), and *Holmwoodinium* sp. cf. *H. notatum* Batten 1985 which appear in low-salinity to freshwater assemblages in the Lower Cretaceous of Great Britain (Batten, 1985). Dinocysts type P may be compared also with the cysts of *Peridinium* Ehrenberg 1832 from sedimentary sequences in southeastern Buenos Aires Province, related to the Holocene transgression (Borel *et al.,* 2003; Borel, 2007).

Scarce specimens of ?*Morkallacysta* Harris 1974 were recorded in the upper part of the section exhibiting clear palaeoperidinioid archeopyle (1I3P) (Guler *et al.*, 2014: figs. 5.5 and 5.7–9). These non-marine dinoflagellate cysts were originally described for the Paleocene of Australia with a triangular archeopyle (Harris, 1974). A taxonomic revision is necessary to consider the classification of this taxon.

More diversity in La Colonia water bodies: zooplanktonic eggs. Other organic-walled microfossils with complex walls conformed by numerous cell-like elements and with a longitudinal dehiscence suture (Fig. 4.16–20) complete in low proportions (<2 %) the assemblages. These conspicuous palynomorphs are attributed to the form-genus *Schizosporis reticulatus* Cookson and Dettmann 1959. Its dehiscence suture has been commonly interpreted as a diagnostic feature of the Zygnemataceae zygospores (Grenfell, 1995). However, aquatic invertebrates such as rotifer of the Monogononta Class produce diapause eggs with a similar slit suture. Moreover, zygospores do not have walls with cell-like units whereas this is a characteristic of the rotifer eggs of the several genera. In particular, *Hexarthra mira* Hudson, 1871 produce eggs that equate to the microfossils of the form taxon *Schizosporis reticulatus* (Van Geel, 1998).

Resting eggs of invertebrates (including rotifers) have been mentioned and illustrated in Holocene palynological studies of fresh to brackish environments in several sites (Van Geel, 2001; Head *et al.*, 2003; Borel, 2007). These eggs can survive in the sediments until favorable conditions re-occur and constitute a survival strategy in ephemeral water bodies subjected to seasonal dry periods. In particular, rotifers constitute a diverse and abundant zooplanktonic group in shallow lakes, although some of them also have an important role developing in the periphyton at the vegetated littoral zones. *Hexarthra mira* and other species of this genus are known from the Neotropical region of South America (Turner, 1987) and they are warmth-demanding planktonic organisms (Van Geel, 1998).

Palaeoenvironmental interpretation. Three major groups of palynological assemblages were identified based on both species composition and relative frequencies for the San Miguel section (Guler *et al.*, 2014). Productive palynological samples show a gradient from phytoplankton assemblages dominated by brackish water dinoflagellate cysts to fully freshwater planktonic assemblages at the uppermost part of the deposits (Fig. 3).

Pseudopediastrum spp., *Botryococcus* spp. and *Ovoidites* spp. were the dominant components of the palynomorph Groups 2 and 3 (Fig. 3), in the middle and uppermost part of San Miguel section respectively. The abundance of these non-marine algae, together with Dinocysts type P and scarce specimens of the non-marine ?*Morkallacysta* spp. (Fig. 3, Group 2), reveal the existence of low-salinity or low-salinity to freshwater bodies associated to mixed and mudflat environments (see Fig. 2). The green algae are well preserved suggesting they were deposited *in situ* or after minimal transport, representing environments with low energy fluxes. The nearby presence of marshy vegetated areas is shown by the important values of pollen of *Classopollis* Pflug 1953. Water ferns are represented by spores of aquatic bryophytes (Ricciaceae), whereas pterydophyte spores and pollen grains related to Proteaceae, Arecaceae, Liliaceae, Gunneraceae and Podocarpaceae are subordinated (Guler *et al.*, 2014).

In the uppermost part, planktonic assemblages are almost entirely composed by *Pseudopediastrum* spp. and *Botryococcus* spp., and by low proportions of zygnematacean spores, rotifer eggs and *?Vesperopsis* sp. (Fig. 3, Group 3). In agreement, an increase in the frequencies of freshwater aquatic pteridophytes (massulae with microspores of Salviniaceae) is observed. This assemblage is associated with massive mudstones (Fig. 2) and reflects freshwater bodies linked to a supratidal environment, without tidal influence.

Reduced salinity conditions and/or salinity-related changes to a shallow marine coastal environment were also suggested for the basal part of the San Miguel section (Guler *et al.*, 2014). The association is strongly dominated by an almost monotypic assemblage of palaeoperidinioid cysts, denoting salinity-related stressed water conditions, and freshwater green microalgae are practically absent.

The predominance of fine-grained textures –mainly mudstones– throughout the San Miguel section, but particularly true toward the top is associated to low-energy depositional processes, suggesting environments dominated by settling and flocculation from suspension. This may imply brackish water conditions related to coastal environments relatively isolated or disconnected from the direct open-marine influence. Furthermore, the changes in the palynomorph content is consistent with the facies associations interpretation throughout the La Colonia Formation in the Telsen area, from which shallowing-upward trend indicates a progressive shifting of the shoreline basinward, related to highstand progradation of an estuarine-like mosaic with complex brackish to freshwater intertidal lagoons and ponds (Navarro, 2012; Navarro *et al.*, 2012).

DISCUSSION AND CONCLUSIONS

By the Late Cretaceous–Paleocene, freshwater dinoflagellates and green algae dominates the planktonic assemblages of the inland water bodies worldwide. Continental phytoplankton only just diversified during the Eocene, with the development of freshwater diatoms and chrysophytes (Martin Closas, 2003). This highlights the relevance of these organic-walled green algae and dinoflagellate cyst analysis from Maastrichtian–Paleocene coastal environments.

Several palynological studies carried out in Mid to Late Holocene estuarine deposits of Pampean coast revealed the potential of green algae and dinoflagellate cysts as palaeobioindicators (Borel, 2007; Vilanova *et al*., 2006; Mourelle *et al*., 2015). These palynological spectra indicate the occurrence of coastal water bodies showing its physical-chemical variability caused by sea-level changes during the Holocene transgressive-regressive event in the studied coastal sites of Pampa grasslands. Comparison to other proxies (diatoms, pollen and gastropods) enhanced the value of the green algae and non-marine dinoflagellate cysts in the palaeoenvironmental reconstructions of those Holocene sequences. Palynological similarities between these modern-Holocene coastal systems and the ancient coastal setting of the La Colonia Formation were noticed and properly applied in this study. It seems a fundamental tool to unravel the environmental trend through the Maastrichtian–?Paleocene marginal deposit of Patagonia.

In summary, the palynological content of the fine-grained deposits of La Colonia Formation at the San Miguel section in the Telsen area reveals productive and shallow ancient coastal ecosystems with variable salinity conditions. The variation in the composition and proportions of the non-marine aquatic palynomorphs, mainly green microalgae and dinoflagellate cysts, allowed characterizing the different low-salinity water bodies developed in an intertidal flat setting. Changes in the palynological algal composition, along with sedimentological analysis, leads to the characterization of the depositional setting and palaeoenvironmental shifts in the San Miguel section of the La Colonia Formation.

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LIST OF IDENTIFIED PLANKTONIC TAXA

Green algae

Division CHLOROPHYTA (Pascher) *emend*. Lewis and McCourt 2004
Class CHLOROPHYCEAE (Kützing) Christensen 1994
Order SPHAEROPLEALES Deason *et al*. 1991
Family HYDRODICTYACEAE Dumortier 1829 *emend*. Deason *et al*. 1991
Genus *Pseudopediastrum* Hegewald 2005 (in Buchheim *et al*. 2005)
Pseudopediastrum brevicorne (Braun) Jena and Bock 2014
Pseudopediastrum boryanum var. *boryanum* (Turpin) Hegewald 2005
Pseudopediastrum sp.
Class TREBOUXIOPHYCEAE Friedl 1995
Order TREBOUXIALES Friedl 1995
Family BOTRYOCOCCACEAE Wille 1909
Genus *Botryococcus* Kützing 1849
Botryococcus spp.
Division CHAROPHYTA (Karol *et al*.) *emend*. Lewis and McCourt 2004
Class CONJUGATOPHYCEAE Engler 1892
Order ZYGNEMATALES Borge and Pascher 1913
Family ZYGNEMATACEAE (Meneghini) Kutzing 1843
Form-genus *Ovoidites* (Potonié) Krutzsch 1959
Ovoidites grandis (Pocock) Zippi 1998
Ovoidites parvus (Cookson and Detmann) Nakoman 1966
Division DINOFLAGELLATA (Bütschli) Fensome *et al*. 1993
Class DINOPHYCEAE Pascher 1914
Order PERIDINIALES Haeckel 1894
Suborder PERIDINIINEAE (Autonym)
Family PERIDINIACEAE Ehrenberg 1831
Subfamily PALAEOPERIDINIOIDEAE (Vozzhennikova) Bujak and Davies 1983
Genus *Ginginodinium* Cookson and Eisenack, *emend*. Lentin and Williams 1976
?*Ginginodinium* sp.
Subfamily INCERTA
Dinocyst type P
Subfamily INCERTA
Genus *Morkallacysta* Harris 1974
?*Morkallacysta* spp.
Suborder CERATIINEAE Fensome *et al*. 1993
Family CERATIACEAE Willey and Hickson 1909
Genus *Vesperopsis* Bint *emend*. Mao *et al*. 1999
?*Vesperopsis* sp.

Invertebrate zooplankton

Phylum ROTIFERA Cuvier, 1817
Class MONOGONONTA Plate, 1889
Order Flosculariacea Harring, 1913
Family Hexarthridae Bartos, 1959
Genus *Hexarthra* Schmarda, 1854
Hexarthra mira Hudson, 1871

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EARLY CRETACEOUS DINOFLAGELLATE CYSTS FROM THE NEUQUÉN AND AUSTRAL BASINS: A REVIEW

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Abstract. The present work documents and gathers the most relevant records of the organic-walled dinoflagellate cysts from different sites of the Neuquén and Austral Basins. Most of these records have contributed to the palaeoenvironmental, biostratigraphical and palaeobiogeographical interpretations of the different stratigraphical units in both basins. The dinoflagellate cysts assemblages come from the Springhill, Upper Río Mayer, Piedra Clavada, Kachaike and "Margas Verdes" Formation of the Austral Basin, and from the upper part of the Vaca Muerta and the Agrio Formations of the Neuquén Basin, several of these stratigraphical units conform the main petroleum systems in both basins.

Key words. Cretaceous. Marine palynomorphs. Sedimentary basins. Argentina.

Resumen. QUISTES DE DINOFLAGELADOS DEL CRETÁCICO TEMPRANO DE LAS CUENCAS NEUQUINA Y AUSTRAL: UNA REVISIÓN. Se documentaron y recopilaron los registros más relevantes de los quistes de dinoflagelados de pared orgánica provenientes del Cretácico Inferior de las cuencas Neuquina y Austral en diferentes localidades de estudio. La mayoría de estos registros han contribuido a las interpretaciones paleoambientales, bioestratigráficas y paleobiogeográficas de diferentes sucesiones sedimentarias marinas en ambas cuencas. Las asociaciones de quistes de dinoflagelados provienen de las Formaciones Springhill, Río Mayer Superior, Piedra Clavada, Kachaike y "Margas Verdes" de la Cuenca Austral, y de la parte superior de las Formaciones Vaca Muerta y Agrio de la Cuenca Neuquina, varias de estas unidades estratigráficas conforman los principales sistemas petroleros de ambas cuencas.

Palabras clave. Cretácico. Palinomorfos marinos. Cuencas sedimentarias. Argentina.

ORGANIC-WALLED marine dinoflagellate cysts have offered valuable bioestratigraphic information for the Lower Cretaceous Basins from the Boreal (*e.g.,* Prössl, 1990; Williams *et al.*, 1990; Harding, 1990; Nør-Hansen, 1993) and Mediterranean Realms (*e.g.,* Leereveld, 1997a,b; Torricelli, 2000), as well as in the Southern Hemisphere in Australia (Helby *et al.,* 1987; Oosting *et al.*, 2006) and Antartica (Riding and Crame 2002). In southernmost South America, dinoflagellate cysts have contributed to elucidate biostratigraphic and palaeobiogeographic aspects in the Austral Basin (*e.g.,* Palamarczuk *et al.*, 2000a,b; Guler *et al.*, 2003; Guler and Archangelsky, 2006) and the Neuquén Basin (*e.g.,* Peralta, 1997; Volkheimer, 2010; Guler *et al.*, 2013), the two most important oil-producing basins from Argentina and Chile.

The Austral Basin is limited by the Southern Patagonian Andes to the west and by the Deseado Massif to the east (Biddle *et al.*, 1986; Robbiano *et al.*, 1996). It includes about 8000-m-thick deposits ranging from the Late Jurassic to the Cenozoic (*e.g.*, Schwarz *et al.*, 2011). During the Early Cretaceous, a regionally extended succession, mostly composed of marine fine sediments, was deposited in a sagging phase (Biddle *et al.*, 1986; Robbiano *et al.*, 1996). The Springhill Formation and its equivalents (lower Río Mayer and the subsurface "Lower *Inoceramus*" Formations) represent the oldest sedimentary rocks of the Austral Basin, which were deposited mostly during Berriasian–Barremian times. They represent a long-term (>25 My) transgressive cycle likely controlled by low-frequency sea-level fluctuations in a back arc setting (*e.g.*, Biddle *et al.*, 1986; Robbiano *et al.*, 1996; Arbe and Fernández Bell Fano, 2002), commonly developed as the infill of extensive topographic depressions (Schwartz *et al.*, 2011). The Aptian to Albian upper part of the Río Mayer

Formation, the equivalent Kachaike Formation and the subsurface deep marine "Margas Verdes" unit, were accumulated at the end of this thermal subsidence phase.

The Neuquén Basin is located in central-western Argentina between 32°–40° South Latitudes and covers part of the Mendoza, Neuquén, Río Negro and La Pampa provinces. The infill of the Basin comprises more than 7000 m of marine and continental sedimentary rocks, ranging in age from the Late Triassic to the Paleocene (Legarreta and Gulisano, 1989; Legarreta and Uliana, 1991). It is a major Mesozoic to Neogene depocenter, and one of the few Southern Hemisphere basins having an excellent marine record from latest Jurassic to mid Early Cretaceous (early Barremian) times. During that interval, the area formed a back-arc basin linked to the Pacific Ocean on its western margin through a volcanic island arc (Legarreta and Uliana, 1991). It is limited by cratonic areas to the northeast (Sierra Pintada System) and southeast (North Patagonian Massif). During the Early Cretaceous, the basin formed large marine embayments linked to episodes of relative sea level rise (Legarreta and Gulisano, 1989). The marine sedimentary rocks accumulated during the Early Cretaceous (Berriasian–early Barremian) are represented by the Vaca Muerta and Agrio formations of the Mendoza Group (Groeber, 1946). The thick and laterally continuous exposures, and the abundant fossil record of these deposits, make the Neuquén Basin an excellent site for stratigraphic, palaeontological and geochemical studies.

The aim of this work is to review and summarize the most relevant biostratigraphical and palaeobiogeographical

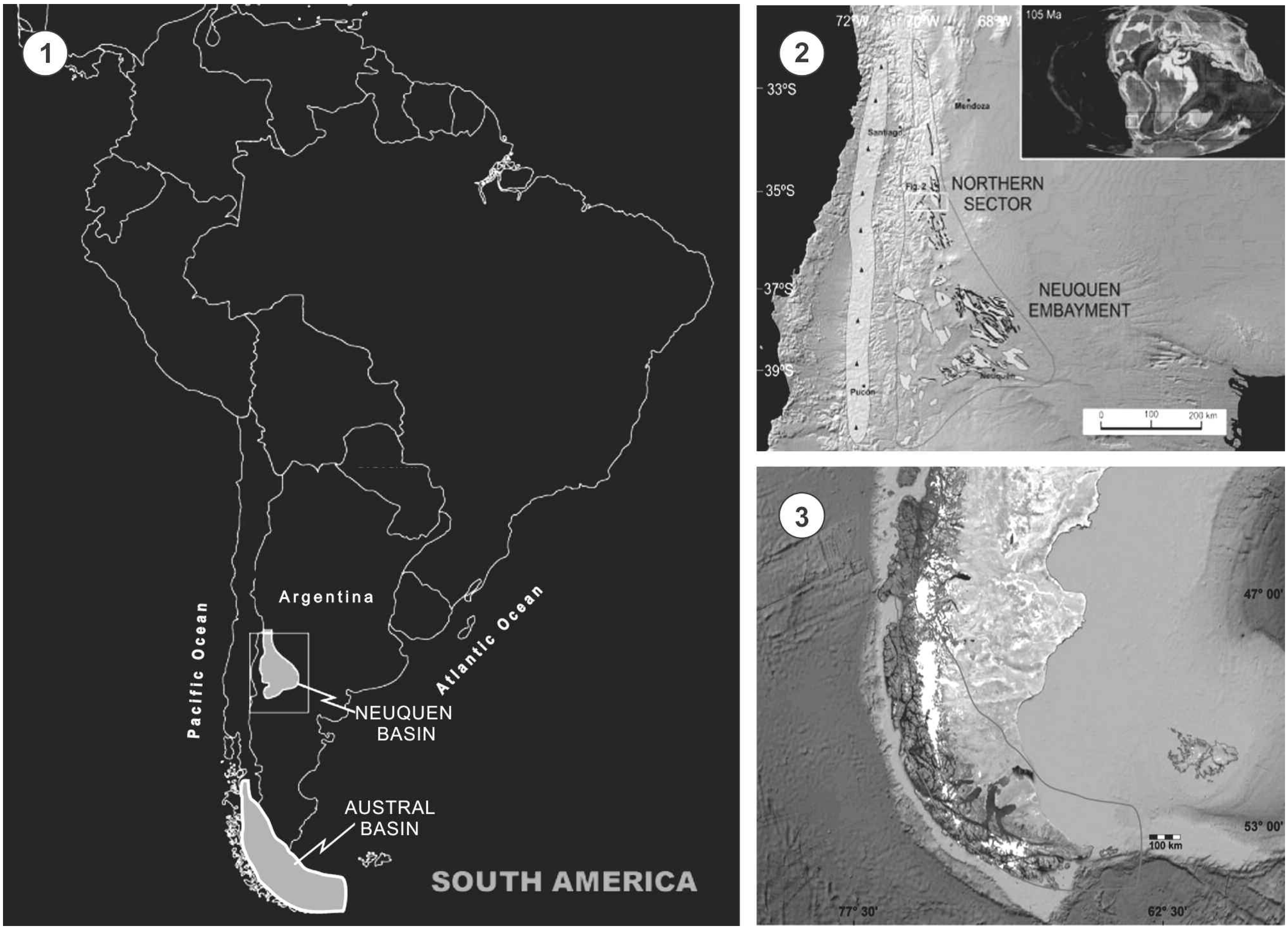


Figure 1. 1, Location map of the Neuquén and Austral Basins in the southernmost part of South America. **2,** Location of the Neuquén Basin in the central-west Argentina. **3,** Location of the Austral Basin in the southern tip of Argentina.

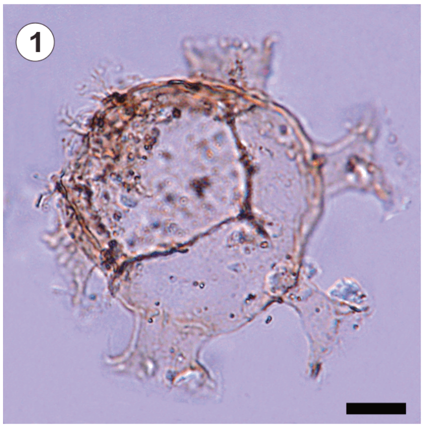
data based on dinoflagellate cysts published to date from Early Cretaceous sedimentary succesions of the Austral and Neuquén basins. Most of the stratigraphical units herein presented include several economically-important hydrocarbon source and reservoir rocks (Uliana and Legarreta, 1993).

SIGNIFICANT EARLY CRETACEOUS DINOFLAGELLATE CYSTS RECORD FROM THE SOUTHERNMOST PART OF SOUTH AMERICA

Neuquén Basin

Palynological studies on Cretaceous deposits of the Neuquén Basin, focused on dinoflagellate cysts, began in the 80's. The oldest records come from the black shales of the Vaca Muerta Formation of early Tithonian–early Valanginian age (Legarreta and Uliana, 1991; Legarreta *et al.*, 1993). Quattrocchio and Volkheimer (1985) documented late Berriasian dinoflagellate cysts in the Mallín Quemado locality, Neuquén province. These authors recognized 12 dinoflagellate cyst taxa including *Gonyaulacysta* sp. A, cf. *Rhaetogonyaulax* sp., *Pareodinia* cf. *P. ceratophora* Deflandre 1947 *emend*. Gocht 1970, *Acanthaulax* sp., *Leptodinium ambiguum* (Deflandre 1939) Helenes 1984, *Ctenidodinium tenellum* Deflandre 1939, *Hystrichosphaerina neuquina* Quattrocchio and Volkheimer 1983 *emend*. Quattrocchio and Sarjeant 1992, *Systematophora* sp. A, *Prolixosphaeridium* sp., *Sentusidinium* sp. A, *Lithodinia* sp. A., and the new species *Cribroperidinium reticulatum* Quattrocchio and Volkheimer 1985. Afterwards, Quattrocchio and Volkheimer (1990) added *Pareodinia ceratophora* var. *pachyceras* (Sarjeant 1959) Lentin and Williams 1973, *Sentusidinium villersense* (Sarjeant 1968) Sarjeant and Stover 1978, and *Systematophora penicillata* (Ehrenberg 1843) Sarjeant 1980 to the previous taxonomic list of the Mallín Quemado locality, and considered *Hystrichosphaerina neuquina* and *Cribroperidinium reticulatum* as endemic species of the Neuquén Basin.

Dinoflagellate cyst assemblages from the late Valanginian–early Hauterivian Pilmatué Member of the Agrio Formation were documented for the first time by Quattrocchio and Volkheimer (1990) at the Pichaihue Abajo, Bajada Vieja and Cerro Mesa localities. More detailed studies of the Pilmatué Member were carried out by Peralta (1997) at the Cerro Mesa and Cerro Negro of Covunco sections (Neuquén province) where they recorded about 42 taxa. With the exception of the gymnodinialean genus *Dinogymnium* Evitt *et al.* 1967 *emend*. Lentin and Vozzhennikova 1990, the species identified belong to the Order Gonyaulacales, chorate and proximochorate cysts (*e.g., Achomosphaera neptuni* (Eisenack 1958) Davey and Williams 1966a, *A. ramulifera* (Deflandre 1937) Evitt 1963, *Kleithriasphaeridium fasciatum* (Davey and Williams 1966b) Davey 1974, *K. simpliscispinum* (Davey and Williams 1966b) Davey 1974, *Oligosphaeridium complex* (White 1842) Davey and Williams 1966b, *Spiniferities ramosus* (Ehrenberg 1838) Mantell 1854, *Surculosphaeridium longifurcatum* (Firtion 1952) Davey *et al*. 1966, *Systematophora rosenfeldii* Volkheimer and Sarjeant 1993, *Tanyosphaeridum variecalamum* (Davey and Williams 1966b); proximate cysts (*e.g.*, *Batiacasphaera asperata* Backhouse 1987, *Cassiculosphaeridia magna* Davey 1974 *emend*. Harding 1990, *Cribroperidinium orthoceras* (Eisenack 1958) Davey 1969 *emend*. Sarjeant 1985, *C. muderongense* (Cookson and Eisenack 1958) Davey 1969, among the most frequent) and cavate cysts with the common presence of *Dingodinium cerviculum* Cookson and Eisenack 1958 *emend*. Khowaja-Ateequzzaman *et al.* 1990 (Peralta, 1997). The relative abundance data of these three morphological groups of cysts contributed to characterize the marine palaeoenvironments which oscillates from external neritic to neritic and coastal environments through the section (Peralta and Volkheimer 1997, 2000). In 2010, Volkheimer described a late Valanginian–early Hauterivian dinoflagellate cyst assemblage from Santa Elena locality, and recognized 30 morphotypes with the definition of two new endemic species for the Member: *Oligosphaeridium quattrocchiae* Volkheimer 2010 and *Muderongia sarjeantii* Volkheimer 2010. Recently, Paolillo *et al*. (2015) identified at the Bajada del Agrio locality, 41 species belonging to the Order Gonyaulacales. Assemblages are dominated by *Cribroperidinium* spp., *Hystrichodinium pulchrum* Deflandre 1935, *Circulodinium distinctum* (Deflandre and Cookson 1955) Jansonius 1986 and *Florentinia* spp. Additionally, three biostratigraphically significant events were identified for the Lower Cretaceous of the Neuquén Basin, that consist of the oldest (first) and/or the youngest (last) occurrence of a particular species, herein referred as “First appearance datums” or FADs and “Last appearance datum” or LADs, respectively. These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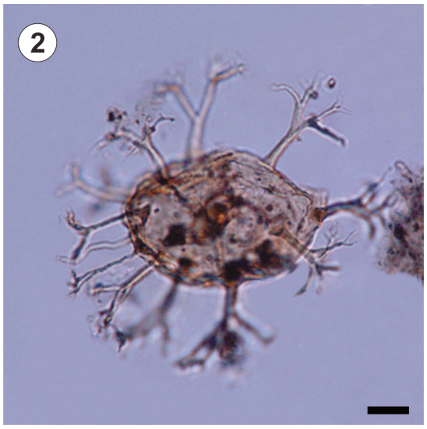
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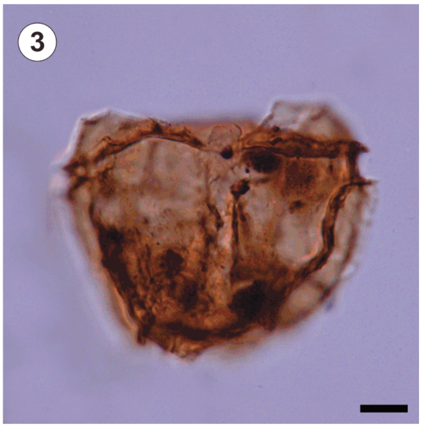
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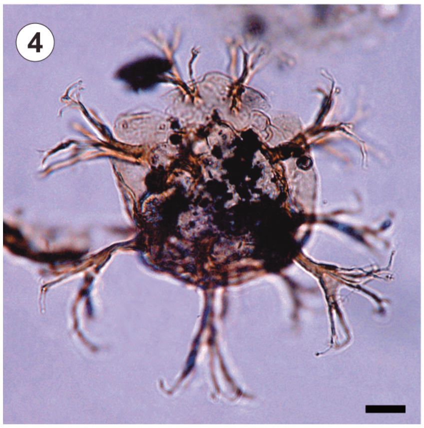
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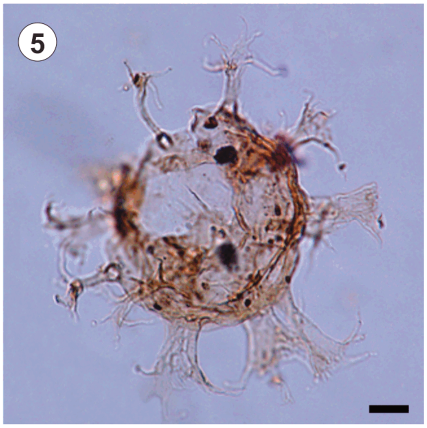
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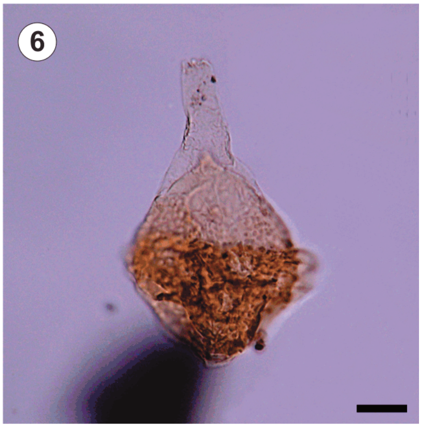
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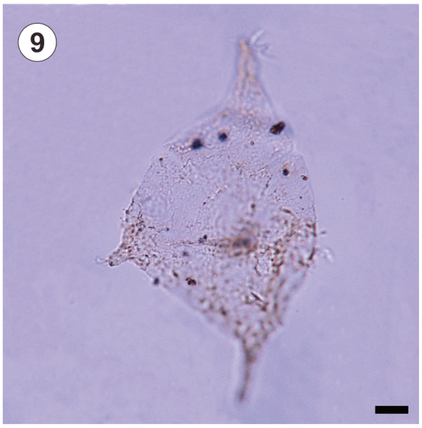
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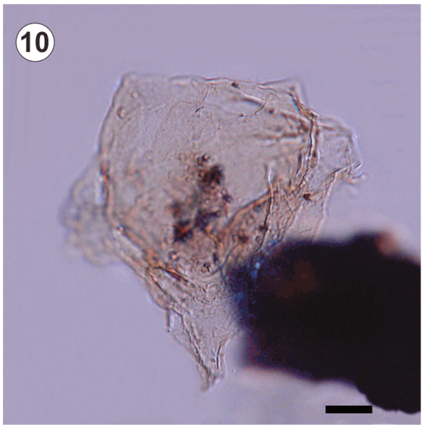
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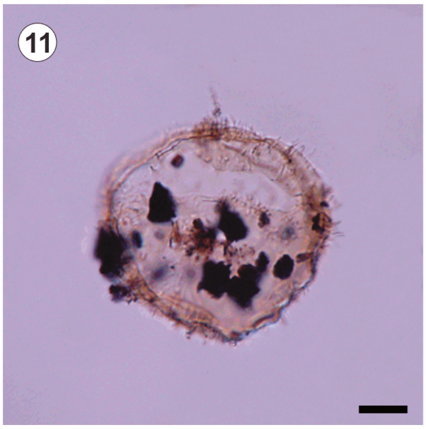
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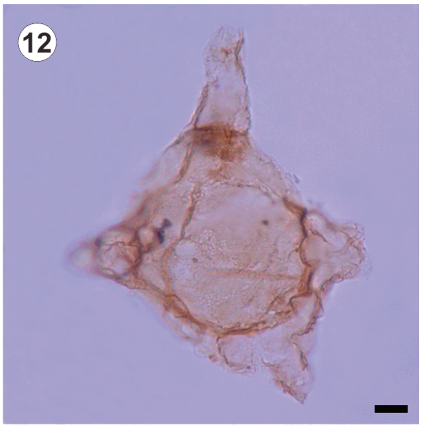
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events are the FAD of *Callaiosphaeridium asymmetricum* (Deflandre and Courteville 1939) Davey and Williams 1966b *emend*. Clarke and Verdier 1967, the FAD and the LAD of *Cymososphaeridium validum* Davey 1982. The FAD of *Callaiosphaeridium asymmetricum* was recorded at the base of the *Holcoptychites neuquensis* Subzone of the *H. neuquensis* Zone of Aguirre Urreta and Rawson (1997), assigned to the earliest Hauterivian. The FAD of *Cymososphaeridium validum* was identified at the uppermost part of the *Hoplitocrioceras gentilii* Subzone of the *H. gentilii* Zone of Aguirre Urreta and Rawson (1997), dated as late early Hauterivian, and the LAD of this species was recorded at the lower part of the *Crioceratites diamantensis* Zone of Aguirre Urreta and Rawson (1997), of a late Hauterivian age.

The first study on dinoflagellate cysts from the Agua de la Mula Member was carried out at the Agua de la Mula and Bajada del Agrio sections by Hernández *et al*. (2005) and Ottone *et al*. (2008). The gonyaulacalean *Circulodinium distinctum*, *Cribroperidinium orthoceras*, *Cribroperidinium spp.*, *Exochosphaeridium bifidum* (Clarke and Verdier 1967) Clarke *et al*. 1968, *Florentinia mantellii* (Davey and Williams 1966b) Davey and Verdier 1973, *Florentinia* spp., *Kiokansium unituberculatum* (Tasch in Tasch *et al.* 1964) Stover and Evitt 1978, *Hystrichodinium pulchrum* and *Oligosphaeridium complex* are the dominant taxa in these assemblages and particularly, ceratiacean morphotypes such as *Phoberocysta neocomica* (Gocht 1957) Millioud 1969 *emend*. Helby 1987, *Muderongia staurota* Sarjeant 1966 *emend*. Monteil 1991b, *M. pariata* Duxbury 1983 *emend*. Monteil 1991b and other closely related forms are well represented. Besides the presence of the endemic *Oligosphaeridium quattrocchioae*, most of the species recovered are cosmopolitan such as *Circulodinium distinctum*, *Cribroperidinium* spp., *Exochosphaeridium* spp., *Kiokansium unituberculatum*, *Dingodinium cerviculum* and *Oligosphaeridium complex*, which are present in almost all the assemblages throughout the Agua de la Mula Member. Ceratiacean cysts are represented by *Phoberocysta neocomica, Pseudoceratium pelliferum* Gocht 1957 *emend*. Dörhöfer and Davies 1980 and several morphotypes of the genus *Muderongia* Cookson and Eisenack 1958, mainly *M.* cf. *M. staurota*, *M. pariata*, *M tomaszowensis* Alberti 1961 *emend*. Riding *et al*. 2001, *M*. cf. *M. siciliana* Torricelli 1997, and *M. tetracantha* (Gocht 1957) Alberti 1961 *emend*. Monteil 1991b (Hernández *et al*., 2005; Ottone *et al*., 2008; Guler *et al*., 2013; Paolillo, personal observation). Ottone and Pérez Loinaze (2002) erected a new species *Muderongia brachialis* from the Agua de la Mula Member at Paraje El Rincón (Río Agrio). It is a biostratigraphycally useful taxon within the Neuquén Basin, since its occurrence is restricted to the *Spitidiscus ricardii* and *Crioceratites schlagintweiti* ammonite Zones, which spans the latest early Hauterivian to the base of the late Hauterivian.

Table 1 contains the dinoflagellate cyst species identified in the Neuquén Basin and referenced according to the Fensome and Williams Index; Fensome and Williams (2004).

Austral Basin

Early Cretaceous dinoflagellate cyst assemblages recorded in the marine deposits of the Austral Basin, mainly come from the offshore subsurface sequences, whereas studies in continental areas of Patagonia are scarce. Based on dinoflagellate cysts and ammonites, Pöthe de Baldis and Ramos (1983, 1988) analized Aptian dinoflagellate cysts from the west of Santa Cruz Province, and Ottone and

Figure 2. Early Cretaceous dinoflagellate cysts from the Pilmatué and Agua de la Mula Members of the Agrio Formation, Neuquén Basin. **1,** ***Callaiosphaeridium asymmetricum*** (Deflandre and Courteville) Davey and Williams *emend*. Clarke and Verdier, apical view, low focus BA 4218 35/118,5. **2,** ***Cymososphaeridium validum*** Davey, lateral view, intermediate focus BA 4229 46,5/100. **3,** ***Meiourogonyaulax stoveri*** Millioud, ventral view, high focus BA AG3d 50/103. **4,** ***Surculosphaeridium longifurcatum*** (Firtion) Davey *et al*., dorsal view, low focus BA 4229 37,5/109. **5,** ***Oligosphaeridium quattrocchioae*** Volkheimer, apical view, high focus BA AG3d 29/108,5. **6,** ***Dingodinium cerviculum*** Cookson and Eisenack *emend*. Mehrota and Sarjeant, general view BA AG5b 51/104. **7,** ***Oligosphaeridium complex*** (White) Davey and Williams, oblique apical view, low focus BA 4227 47/108,5. **8,** ***Phoberocysta neocomica*** (Gocht) Helby, dorsal view, low focus BA 4227 54/116,5. **9,** ***Pseudoceratium pelliferum*** Gocht *emend.* Dörhöfer and Davies, ventral view, cross section BA 4211 19/110,5. **10,** ***Muderongia pariata*** Duxbury *emend.* Monteil, dorsal view, low focus BA AG10b 35/120. **11,** ***Nexosispinum*** sp. dorsal view, high focus BA AG21a 37,5/117. **12,** ***Muderongia* cf. *M. tomaszowensis*** Alberti *emend.* Monteil, ventral view high focus BA 4227 20,5/121,5. Scale bar= 10μm.

TABLE 1 – List of the dinoflagellate cyst taxa identified from the Early Cretaceous assemblages of the Neuquén and Austral Basins.

Taxa	*Neuquén Basin*	*Austral Basin*
Acanthaulax sp.	x	
Achomosphaera neptuni *(Eisenack 1958) Davey and Williams 1966a*	x	
A. ramulifera *(Deflandre 1937) Evitt 1963*	x	
Batiacasphaera asperata *Backhouse 1987*	x	
Callaiosphaeridium asymmetricum *(Deflandre and Courteville 1939) Davey and Williams 1966b* emend. *Clarke and Verdier 1967*	x	
Canninginopsis denticulata *Cookson and Eisenack 1962*		x
Cassiculosphaeridia magna *Davey 1974* emend. *Harding 1990*	x	x
Chichaouadinium boydii *(Morgan 1975) Bujak and Davies 1983*		x
Circulodinium distinctum (*Deflandre and Cookson 1955) Jansonius 1986*	x	x
Cometodinium *cf.* **C. comatum** *Srivastava 1984* emend. *Monteil 1991a*		x
Cribroperidinium confossum *(Duxbury 1977) Helenes 1984*		x
C. muderongense *(Cookson and Eisenack 1958) Davey 1969*	x	
C. orthoceras *(Eisenack 1958) Davey 1969* emend. *Sarjeant 1985*	x	
C. reticulatum *Quattrocchio and Volkheimer 1985*	x	
Ctenidodinium tenellum *Deflandre 1939*		x
Cyclonephelium vannophorum *Davey 1969*		x
Cymososphaeridium validum *Davey 1982*	x	
Dingodinium cerviculum *Cookson and Eisenack 1958* emend. *Kowaja-Ateequzzaman* et al. *1990*	x	x
Dinogymnium *Evitt* et al. *1967* emend. *Lentin and Vozzhennikova 1990*	x	
Dinopterygium tuberculatum *(Eisenack and Cookson 1960) Stover and Evitt 1978*		x
Exochosphaeridium bifidum *(Clarke and Verdier 1967) Clarke* et al. *1968*	x	
Florentinia mantellii *(Davey and Williams 1966b) Davey and Verdier 1973*	x	
Gonyaulacysta *sp. A.*	x	
Hapsocysta peridictya *(Eisenack and Cookson 1960) Davey 1979* emend. *Davey 1979*		x
Herendeenia postprojecta *Stover and Helby 1987*		x
Hystrichodinium pulchrum *Deflandre 1935*	x	
Hystrichosphaerina neuquina *Quattrocchio and Volkheimer 1983* emend. *Quattrocchio and Sarjeant 1992*	x	
Kaiwaradinium scrutillinum *Backhouse 1987*		x
Kiokansium unituberculatum *(Tasch in Tasch* et al. *1964) Stover and Evitt 1978*	x	
Kleithriasphaeridium fasciatum *(Davey and Williams 1966b) Davey* 1974	x	x
K. simpliscispinum *(Davey and Williams 1966b) Davey 1974*	x	
Leptodinium ambiguum *(Deflandre 1939) Helenes 1984 (as Millioudodinium ambiguum*)	x	

Table 1 – Continuation.

Taxa	*Neuquén Basin*	*Austral Basin*
Lithodinia *sp. A*	*x*	
Litosphaeridium arundum *(Eisenack and Cookson 1960) Davey 1979* emend. *Lucas-Clark 1984*		*x*
Muderongia brachialis *Ottone and Pérez Loinaze 2002*	*x*	
M. pariata *Duxbury 1983* emend. *Monteil 1991b*	*x*	
M. sarjeantii *Volkheimer 2010*	*x*	
M. staurota *Sarjeant 1966* emend. *Monteil 1991b*	*x*	
M. *cf.* **M. staurota** *Sarjeant 1966* emend. *Monteil 1991b*	*x*	
M. tetracantha *(Gocht 1957) Alberti 1961* emend. *Monteil 1991b*	*x*	*x*
M. tomaszowensis *Alberti 1961* emend. *Riding* et al. *2001*	*x*	
M. *cf.* **M. siciliana** *Torricelli 1997*	*x*	
Nematosphaeropsis densiradiata *(Cookson and Eisenack 1962b) Stover and Evitt 1978*		*x*
Odontochitina operculata *(Wetzel 1933) Deflandre and Cookson 1955*		*x*
Oligosphaeridium complex *(White 1842) Davey and Williams 1966b*	*x*	*x*
O. quattrocchiae *Volkheimer 2010*	*x*	
O. pulcherrimum *(Deflandre and Cookson 1955) Davey and Williams 1966b*		*x*
Ovoidinium cinctum *(Cookson and Eisenack 1958) Davey 1970*		*x*
Pareodinia *cf.* **P.ceratophora** *Deflandre 1947* emend. *Gotch 1970*	*x*	
Pareodinia ceratophora var. pachyceras *(Sarjeant 1959) Lentin and Williams 1973*	*x*	
Phoberocysta neocomica *(Gocht 1957) Millioud 1969* emend. *Helby 1987*	*x*	*x*
Prolixosphaeridum conulum *Davey 1969*		*x*
P. parvispinum *(Deflandre 1937) Davey* et al. *1969*		*x*
Prolixosphaeridium *sp.*	*x*	
Pseudoceratium pelliferum *Gocht 1957* emend. *Dörhöfer and Davies 1980*	*x*	
Senoniasphaera tabulata *Helby 1987*		*x*
Sentusidinium villersense *(Sarjeant 1968) Sarjeant and Stover 1978*	*x*	
Sentusidinium *sp. A*	*x*	
Spiniferities ramosus *(Ehrenberg 1838) Mantell 1854*	*x*	
Surculosphaeridium longifurcatum *(Firtion 1952) Davey* et al. *1966*	*x*	
Systematophora penicillata *(Ehrenberg 1843b) Sarjeant 1980*	*x*	
Systematophora rosenfeldii *Volkheimer and Sarjeant 1993*	*x*	
Systematophora *sp. A*	*x*	
Tanyosphaeridum variecalamum *(Davey and Williams 1966b)*	*x*	

References correspond to the Fensome and Williams Index; Fensome and Williams (2004).


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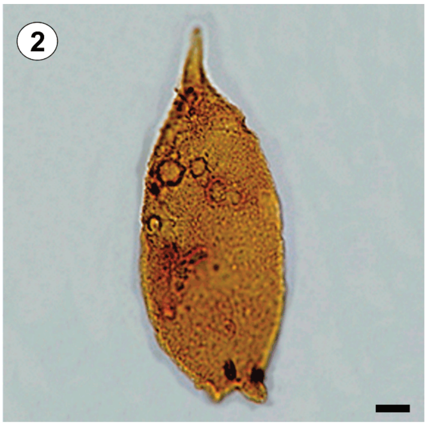
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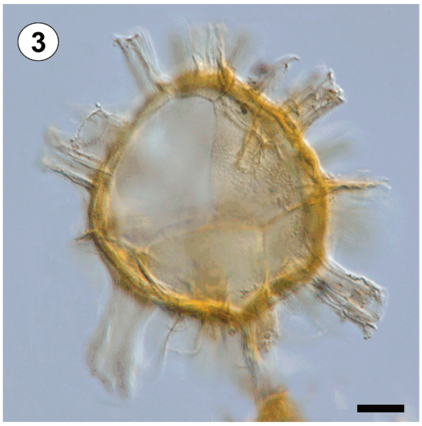
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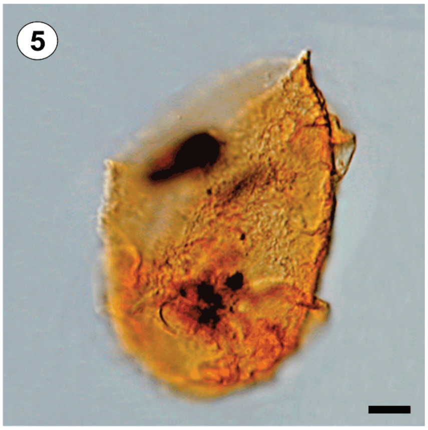
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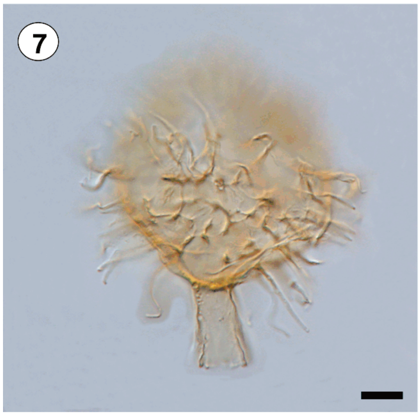
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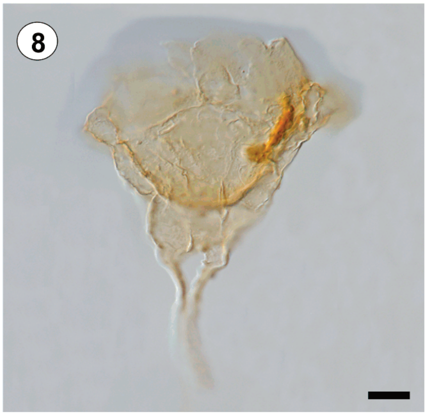
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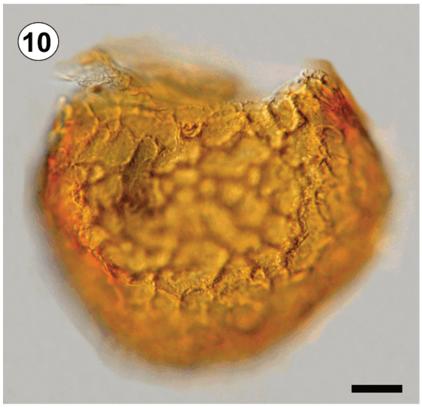
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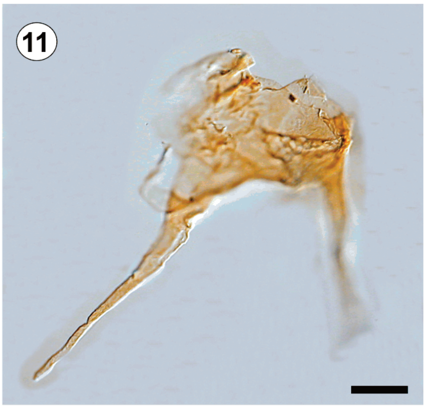
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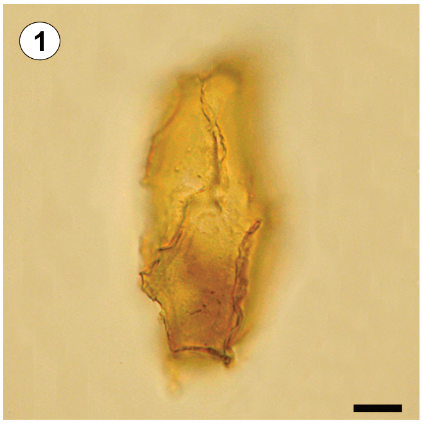
Aguirre Urreta (2000) suggested a probable late early Hauterivian–early Barremian age for the Springhill Formation, at southwestern Santa Cruz Province. Cornú (1986) described the palynoflora from wells sections offshore eastern Tierra del Fuego province and indicates four informal dinoflagellate cyst zones for the upper marine interval of the Springhill and the Lower *Inoceramus* formations. Also, Palamarczuk *et al.* (2000a,b) recognized a late Valanginian–Hauterivian lower marine interval in well sections offshore eastern Santa Cruz.

Offshore northeastern Tierra del Fuego province, Quattrocchio *et al.* (2006) correlated deposits of the Springhill Formation with the *Interulobites-Foraminisporis* Assemblage Zone (upper Valanginian–upper Hauterivian) of Archangelsky *et al.* (1984), defined for the Austral Patagonia, and with the upper Valanginian–lower Aptian *Cyclusphaera psilata-Classopollis* Zone of Volkheimer (1980), for the Neuquén Basin. They recorded a dinoflagellate cyst-dominated palynomorph assemblage composed by *Circulodinium distinctum, Cometodinium* cf. *C. comatum* Srivastava 1984 *emend.* Monteil 1991a, *Cribroperidinium confossum* (Duxbury 1977) Helenes 1984, *Cyclonephelium vannophorum* Davey 1969 and *Oligosphaeridium complex,* suggesting transitional to offshore marine conditions, and other assemblage characterized by *Aptea* spp. and prasinophyceaen algae (*Tasmanites* Newton 1875 and *Pterospermella* Eisenack 1972) indicating brackish-water environments.

Well preserved and moderately diverse dinoflagellate cyst assemblages were recovered from the Springhill Formation in eight wells located offshore southeastern Argentina (Guler *et al.*, 2003; Guler *et al.,* 2015). A sequence of eight age-diagnostic bioevents characterizes the easternmost Early Cretaceous deposits of the Austral Basin. These are, in ascending order: the LAD of *Senoniasphaera tabulata* Helby 1987*,* the LAD of *Kleithriasphaeridium fasciatum*, the FAD of *Prolixosphaeridium parvispinum* (Deflandre 1937) Davey *et al.* 1969*,* the LAD of *Phoberocysta neocomica*, the FAD of *Herendeenia postprojecta* Stover and Helby 1987*,* the FAD of *Odontochitina operculata* (Wetzel 1933) Deflandre and Cookson 1955, the LAD of *Cassiculosphaeridia magna* and the LAD of *Kaiwaradinium scrutillinum* Backhouse 1987. These bioevents constrain the age of the subsurface sections to the late Barremian. Furthermore, it was recognized the upper part of the *Muderongia testudinaria* and the *Muderongia australis* Zones of Helby *et al.* (1987), extending both zones to the beginning of the late Barremian and the early Aptian (Oosting *et al.,* 2006), respectively. Palaeopeoperidiniod cysts-dominated assemblages of cf. *Ovoidinium* sp. were recorded consistently at the top of most of the sequences (Guler *et al.,* 2003, 2015), which presumable represent endemic taxa for the southeastern Atlantic Ocean. An acme of *Ovoidinium cinctum* (Cookson and Eisenack 1958) Davey 1970 mark the *O.* (as *Ascodinium*) *cinctum* Subzone (Helby *et al.*, 1987, 2004) when it is present at the uppermost part of the *M. australis* Zone. Oosting *et al.* (2006) document the consistent presence of *O. cinctum* and recognize the Subzone in the *M. australis* and *O. operculata* Zones, boundary in the earliest Aptian. The late Barremian age proposed for the Springhill Formation is in accordance with the strong diachronism of the unit, being the youngest deposits at the east and north of the basin; the wells are located in front of the southernmost tip of Santa Cruz province, and these

Figure 3. Barremian dinoflagellate cysts from the Springhill Formation, offshore Austral Basin. **1,** ***Dingodinium cerviculum*** Cookson and Eisenack, right lateral view, cross section, BA PB Pal 6301 100.5/44.5 EF J30/4. **2,** ***Batioladinium micropodum*** (Eisenack and Cookson) Brideaux, ventral view, low focus, BA PB Pal 6306 39/106 EF W30. **3,** ***Kleithriaspheridinium fasciatum*** (Davey *et al.*) Davey, oblique ventral view, low focus, BA Pb Pal 6312 24/113 EF M24/3. **4,** ***Muderongia australis*** Helby, dorsal view/low focus, BA Pb Pal 6306 31/99 EFZ31/4. **5,** ***Aprobolocysta* sp. cf. *A. alata*** Backhouse, left lateral view, intermediate, BA PB Pal 6307 29.5/105 EF V29/2. **6,** ***Herendeenia postprojecta*** Stover and Helby, oblique ventral view, cross section, BA PB Pal 6301 23.5/112.5 EF N23. **7,** ***Coronifera oceanica*** Cookson and Eisenack, ventral view, high focus, BA PB Pal 6301 33.5/113 EF N35/1. **8,** ***Muderongia imparilis*** (Duxbury) Bint, dorsal view, high focus, BA PB Pal 6306 47/104 EF W47/4. **9, cf. *Ovoidinium* sp.,** dorsal view, intermediate focus, BA PB Pal 6301 48107.5 EF H48/2. **10,** ***Cassiculosphaeridia magna*** Davey, dorsal view, intermediate focus, BA PB Pal 6312 46.5/117 EF H47/3. **11,** ***Odontochitina operculata*** (Wetzel) Deflandre and Cookson, dorsal view, low focus, 6306 48.9/112 W27. **12,** ***Apteodinium granulatum*** (Eisenack) Lucas-Clark BA Pb Pal ventral view, low focus, BA PB Pal 6306 43/104.5 EF V43/4. Scale bar= 10μm.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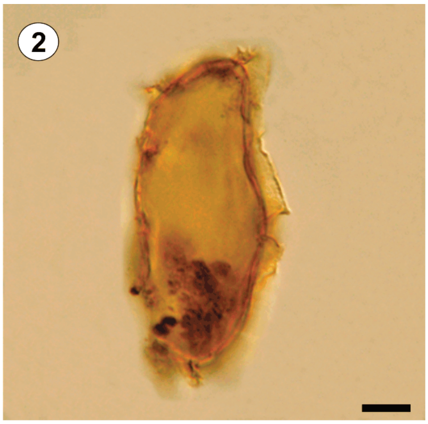
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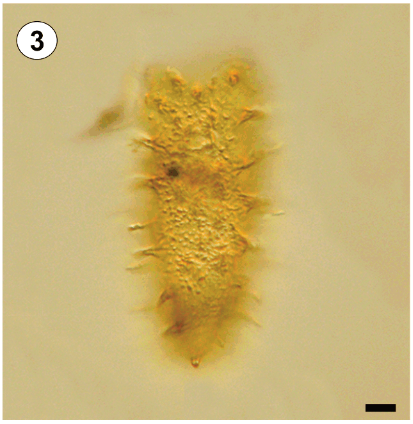
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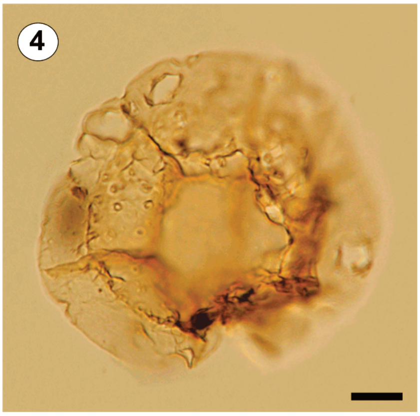
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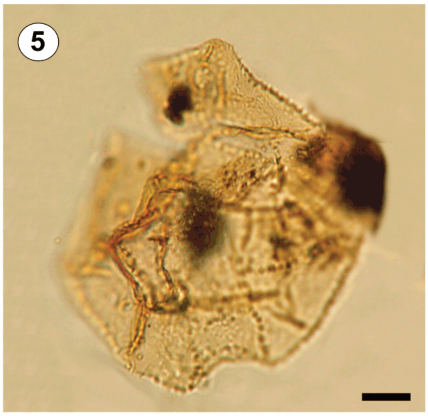
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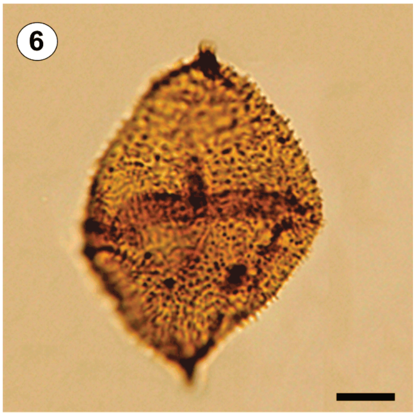
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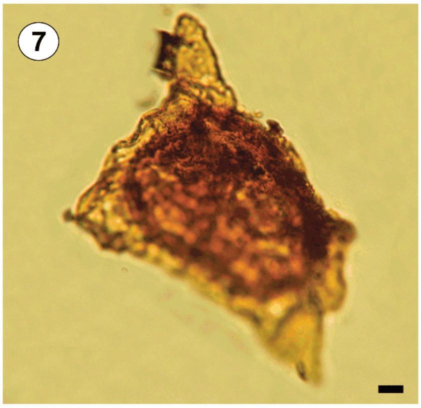
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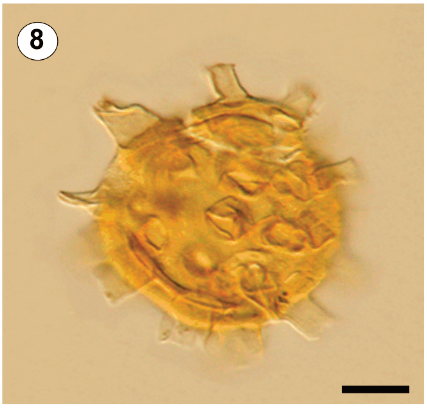
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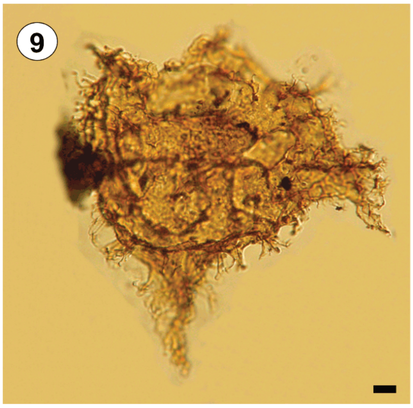
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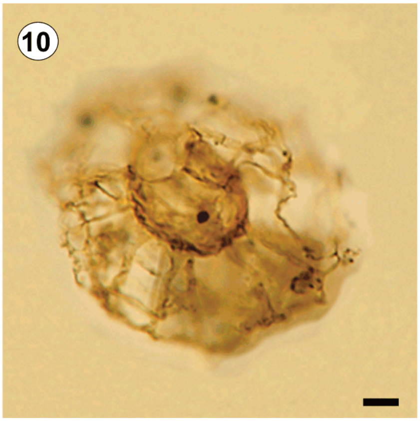
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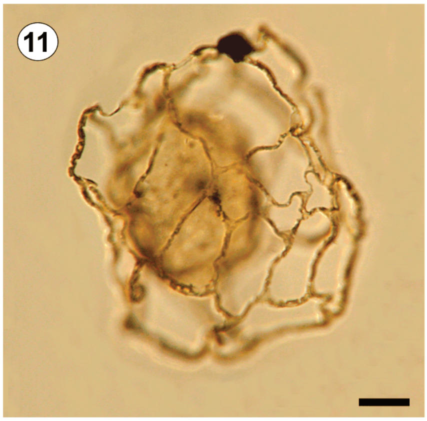
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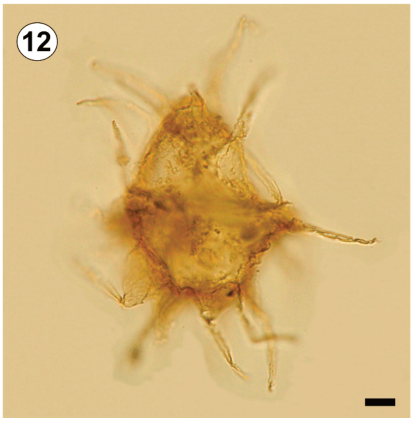
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sequences accumulated in the eastern margin of the basin.

Late Aptian, Albian and early Cenomanian dinoflagellate cyst assemblages were recorded at the uppermost Río Mayer Formation and the overlying Kachaike or the equivalent Piedra Clavada Formations outcrop sections, as well as from the deep marine shales of the "Margas Verdes" Formation in the subsurface deposits. The Kachaike Formation is a typical Albian unit in the southwest of Patagonia at the San Martin lake area, and the uppermost part of the Río Mayer Formation is well-known by its rich fossiliferous content, where marine invertebrates include ammonoids of the Aptian/Albian transition. The FADs of *Litosphaeridium arundum* (Eisenack and Cookson 1960) Davey 1979 *emend*. Lucas-Clark 1984 (Fig. 2.2), *Chichaouadinium boydii* (Morgan 1975) Bujak and Davies 1983, *Prolixosphaeridum conulum* Davey 1969 and *Dinopterygium tuberculatum* (Eisenack and Cookson 1960) Stover and Evitt 1978 and the LAD of *Muderongia tetracantha* constitute key biostratigraphic events and constrain the age of the Kachaike Formation and the coetaneous Piedra Clavada Formation in different sites of southwestern Patagonia (Baldoni *et al.*, 2001; Guler and Archangelsky, 2006; Medina *et al.,* 2008). The underlying uppermost Río Mayer Formation is well-known by their rich fossiliferous content, it is a classical section in the Santa Cruz province where marine invertebrates include ammonoids of the Aptian/Albian transition, whereas the Piedra Clavada Formation is dated as early Albian based on ammonoids of the genus *Beudanticeras* (Medina *et al.,* 2008). The presence of *Dingodinium cerviculum* in these deposits represents the LAD for the species in the Austral Basin, and it is associated with Aptian/Albian transition ammonite fauna; in accordance with the range of the species in Australia which extends into the lowest *Muderongia tetracantha* Zone. It was recognized in these Albian units the Subzone b of *Endoceratium turneri* Zone and the coeval *Muderongia teracantha* Interval Zone of Morgan (1980) and Helby (1987), of early Albian age; the LAD of *Muderongia tetracantha* marks the top of these zones. Subsurface sections of the "Margas Verdes" Formation from the offshore Austral Basin exhibit a complete Albian dinoflagellate cyst event sequences (Palamarczuk *et al.,* 2000a; Guler, personal observation), mostly the last occurrences where the continuous and common occurrence of *Hapsocysta peridictya* (Eisenack and Cookson 1960) Davey 1979 *emend*. Davey 1979 is indicative of a minimum early Albian age. The *H. peridictya* stratigraphic range extends from the top of the Subzone a, to the top of the Subzone b of the *Pseudoceratium turneri* of Morgan (1980), assigned to the early Albian. In Australia, the last occurrences of *H. peridictya* and *M. tetracantha* are simultaneous (Morgan, 1980) and the absence of *M. tetracantha* is presumably due to the deep marine character of these assemblages. In general, in these Albian assemblages, it is common the presence of species of *Diconodinium* Eisenack and Cookson 1960 *emend.* Morgan 1977, *Odontochitina* (mostly *O. costata* Alberti 1961) and *Canninginopsis denticulata* Cookson and Eisenack 1962*.* In turn, those assemblages from deep marine settings are characterized by high proportions of *Impagidinium* Stover and Evitt 1978*, Pterodinium* Eisenack 1958 and chorate cysts like *Oligosphaeridium pulcherrimum* (Deflandre and Cookson 1955) Davey and Williams 1966b, *O. complex, Nematosphaeropsis densiradiata* (Cookson and Eisenack 1962b) Stover and Evitt 1968 and

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Figure 4. Late Aptian–Albian dinoflagellate cysts from the Upper Río Mayer, Kachaike, Piedra Clavada and "Margas Verdes Formations, onshore Austral Basin. **1,** ***Carpodinium granulatum*** Cookson and Eisenack emend. Leffingwell and Morgan, ventral view, **1,** high focus. **2,** cross section PC 05 31/105 N45/4. **3,** ***Prolixosphaeridinium conulum*** Davey, ventral view, high focus, PC 05 T47 EF T47/4. **4,** ***Dinopterygium tuberculatum*** (Eisenack and Cookson) Stover and Evitt, antapical view, intermediate focus, MV 35/114 EF. **5,** ***Canninginopsis denticulata*** Cookson and Eisenack, dorsal view, low focus, MV 23,5/111 EF U53. **6,** ***Diconodinium multispinum*** (Deflandre and Cookson) Eisenack and Cookson, Oblique right lateral view, low focus, MV 31/105 N46/3. **7,** ***Endoceratium ludbrookiae*** Cookson and Eisenack *emend*. Morgan, ventral view, intermediate focus, MV 38/99 H38/2. **8,** ***Litosphaeridium arundum*** (Eisenack and Cookson) Davey *emend*. Lucas-Clarke, dorsal view, high focus, Kch 99 35/101 K41/4. **9,** ***Endoceratium turneri*** (Cookson and Eisenack) Stover and Evitt, dorsal view, low focus, MV 15/114 EF X48. **10,** ***Nematospheropsis densiradiata*** (Cookson and Eisenack) Stover and Evitt, general view, MV 38/110 S38. **11,** ***Hapsocysta peridictya*** Eisenack and Cookson *emend*. Davey, oblique ventral view, high focus, MV 27/108 R50. **12,** ***Hystrichodinium pulchrum*** Deflandre, left lateral view, high focus, PC 27/113 W50/3. Scale bar= 10µm.

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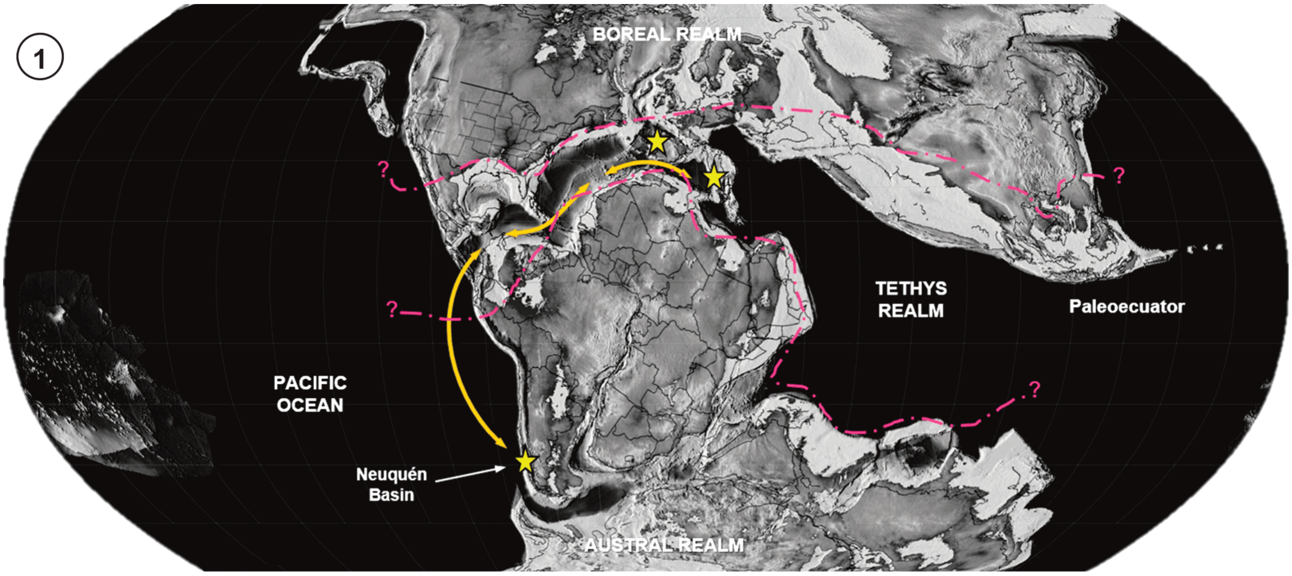
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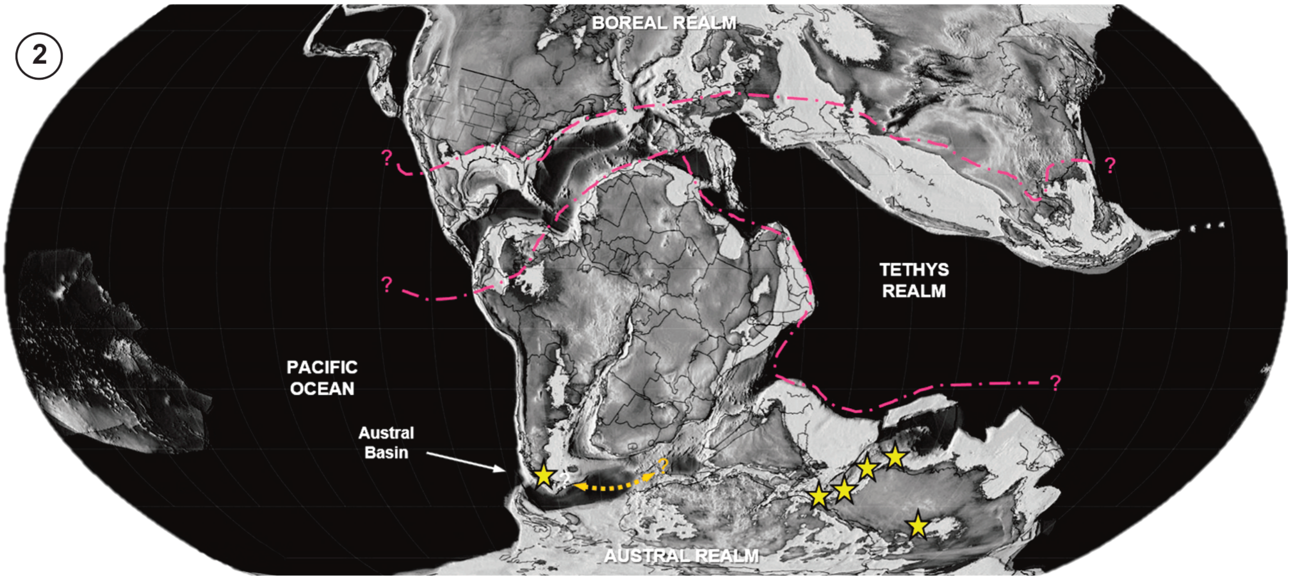
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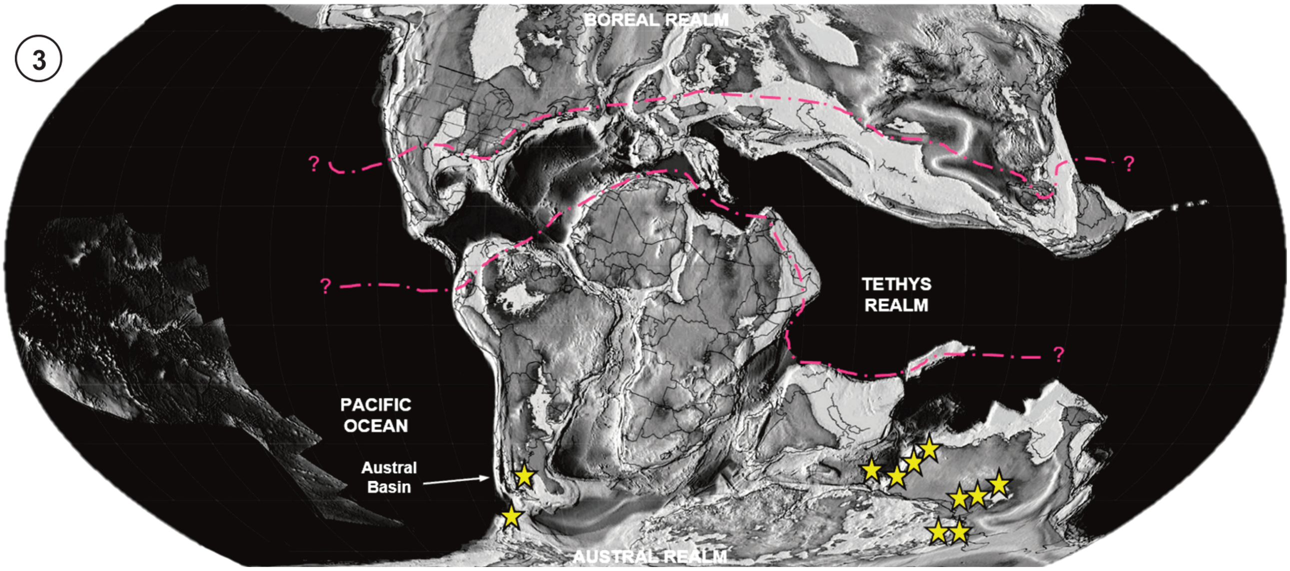
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Hapsocysta peridictya, which are typical oceanic taxa. At the upper part of the sequences it is recognized the middle Albian *C. denticulata*, the late Albian *E. ludbroockiae*, *X. asperatus* and the early Cenomanian *D. multispinum* Zones of Helby *et al.* (1987) and the equivalent subzones of the *E. turneri* and *E. ludbrookiae* Zones of Morgan (1980).

Table 1 contains the dinoflagellate cyst species identified in the Austral Basin referenced according to the Fensome and Williams Index; Fensome and Williams (2004).

PALAEOGEOGRAPHIC AND PALAECOLOGIC IMPLICATIONS FOR THE AUSTRAL AND NEUQUÉN BASINS

In general terms, dinoflagellate cyst assemblages from the Pilmatué Member (Peralta, 1997; Volkheimer, 2010; Paolillo *et al.*, 2015) and the Agua de la Mula Member (Guler *et al.*, 2013) of the Agrio Formation, show similarity with the late Valanginian–late Hauterivian assemblages from the Tethyan Realms (*e.g.,* Leereveld 1997a,b; Torricelli 2000; 2001; 2006).

Otherwise, Early Cretaceous dinoflagellate cysts from the southernmost tip of South America, from offshore Austral Basin and southern Patagonia have strong Austral affinities. It is clear that the Australian palynological zonal schemes of Morgan (1980) and Helby (1987) are applicable to Early Cretaceous deposits of the Austral Basin (*e.g.,* Guler *et al.*, 2003; Guler *et al.*, 2015), providing evidence of palaeobiogeographical affinities with the western and central Australia, mainly during Barremian and Aptian times, when the youngest rocks of the Springhill Formation were accumulated (Fig. 5.2). Mid–Cretaceous assemblages from surface and subsurface deposits of the Austral Basin, including Kachaike, Piedra Clavada and Upper Río Mayer; “Margas Verdes” formations (Medina *et al.*, 2008; Guler and Archangelsky, 2006; Guler, personal observation) compare well with those from well dated sequences of the James Ross Basin, exposed at the north eastern tip of Antarctic Peninsula (Riding and Crame, 2002), which contains one of the thickest and complete Cretaceous sedimentary sequences in the Southern Hemisphere. Also, these Albian–early Cenomanian assemblages are similar to those from Australia (*e.g.,* Morgan, 1980; Helby *et al.*, 1987; Backhouse, 2006) and New Zealand (*e.g.,* Wilson, 1984), reflecting open marine connections among the southernmost part of South America, Antarctic Peninsula, Australia and New Zealand (Fig. 5.3).

Ceratiaceans evolved into a significant number of species through the Early Cretaceous worldwide and they proved to be biostratrigraphically useful in the Boreal and Tethyan Realms (Duxbury, 1977; Leereveld, 1997b; Monteil, 1992) as well as in the Austral region (Helby *et al.*, 1987; Backhouse 1987). The presence of *Muderongia staurota*, *M. pariata*, *M.* cf. *M. siciliana,* and closely related *Muderongia* morphotypes recorded in the Hauterivian of the Neuquén Basin, denote similarity with the Northern Hemisphere. These species of *Muderongia* are conspicuous taxa in the Hauterivian Boreal and Tethyan cyst assemblages (*e.g.*, Duxbury, 1977; Leereveld, 1997b; Torricelli, 2000; 2001; 2006) and are absent in the high-latitude Southern Hemisphere basins. Also, typical austral *Muderongia* species among them *Muderongia australis* Helby 1987, *Muderongia testudinaria* Burger 1980 are index taxa for the Australian zonations (Helby *et al.*, 1987; 2004; Backhouse, 1987) and they were not recorded neither in the Northern Hemisphere nor in the Neuquén Basin.

Furthermore, for the Early Cretaceous, assemblages composed by species of *Aprobolocysta* Duxbury 1977*, Ba-*

Figure 5. 1, Palaeobiogeographic affinities of the late Valanginian–?early Barremian dinoflagellate cysts of the Neuquén Basin. Palaeogeographic reconstruction of the Early Cretaceous showing the main marine connection between the Neuquén Basin and the Tethyan Realm, Western Europe (Leereveld, 1997; Torricelli, 2000; 2001; 2006). **2,** Palaeobiogeographic affinities of the Barremian dinoflagellate cyts of the Austral Basin with the intracratonic areas and marginal basins of Australia (*e.g.*, Helby *et al.*, 1987). Presumable open marine seaways are unknown. **3,** Palaeobiogeographic affinities of the Albian dinoflagellate cyts of the onshore Austral Basin with central and the coastal western Australia (Morgan, 1980; Helby *et al.*, 1987; Backhouse, 2006), New Zealand (Wilson 1984) and Peninsula Antarctica (Riding and Crame, 2002). Base maps by Scotese (2013, PALEOMAP).

tioladinium jaegeri, *B. micropodum*, *Carpodinium granulatum* Cookson y Eisenack 1962, *emend*. Leffingwell y Morgan 1977, *Cassiculosphaeridia magna*, *Dingodinium cerviculum* (large forms with relatively thick walls), among others, were associated with relatively cool waters (De Renéville and Raynaud, 1981; Habib and Drugg, 1987; Leereveld, 1995). Based on these criteria, the dinoflagellate cyst assemblages recorded in the Austral Basin characterized by the common presence of these taxa would reflect cool environments. Large thick-walled and coarse ornamented specimens of *Dingodiniun cerviculum* (Fig 3.1) are common in the Austral Basin assemblages, whereas thin-walled forms (Fig 2.6) were recorded in the Neuquén Basin and other Mediterranean assemblages related to relatively warm environments (Leereveld, 1995, Torricelli 2000, 2001, 2006; Oosting *et al*., 2006).

Thus, Early Cretaceous dinoflagellate cyst assemblages from southern South America, first from the north of Patagonia, have mediterranean affinities reflecting exchange of taxa between the Mediterranean Sea and the Southeastern Pacific Ocean, and then, with the Neuquén Basin (Fig. 5.1), despite the semi enclosed nature of the basin. The palaeo-oceanographical connection between the Neuquén Basin and the northwestern and Western Europe during the late Valanginian–late Hauterivian interval is supported by Early Cretaceous echinoids, ammonoids and bivalves, which also proved that water palaeotemperatures would have been properly high to allow immigration of equatorial faunal components (*e.g*., Aguirre Urreta *et al*., 2008). Instead, assemblages from the Austral Basin suggest oceanic connection between the southernmost tip of South America and other high-latitudes South Hemisphere sites in Australia, New Zealand and Peninsula Antarctica (Figs. 5.2, 3).

In addition to the global palaeogeography and the palaeooceanographic current context, these palaeobiogeographical affinities are closely related to the geodynamic evolution of the both two basins. During the Berriasian–early Barremian, the Neuquén Basin was connected to the Pacific Ocean (Uliana and Biddle, 1988) through a volcanic arc in the western margin, allowing the incoming of thermophilic taxa from the Tethyan region. On the other hand, the oldest sedimentary fill of the Austral basin (Berriasian–Barremian) deposited during the sag phase, represents a long-term (>25 My) transgressive cycle (Robbiano *et al.*, 1996) that is considered contemporary with the initial development of the basin and then, the opening of the Atlantic Ocean (Arbe, 2002). Despite the close palaeogeographical position of both basins, the dinoflagellates cyst assemblages of the Neuquén Basin do not reflect palaeobiogeographic affinities with neither the Austral Basin nor other Southern Hemisphere high latitudes sites, probably due to palaeotemperature differences and/or absence of marine connections.

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JURASSIC ORGANIC-WALLED MARINE MICROPLANKTON FROM THE NEUQUÉN BASIN. DISTRIBUTION, BIOSTRATIGRAPHY AND PALEOBIOGEOGRAPHY. A REVIEW

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Abstract. The Mesozoic Era is crucial for analyzing the replacement of microplanktonic lineages resulting from the beginning of the break-up of Pangea. The paleogeography of South America, and hence of Argentina, underwent successive changes since this time. The opening of different seaways, mainly during the Jurassic, affected the global circulation pattern of the oceans which determined the composition of the organic-walled marine microplankton associations of the Neuquén Basin. These Jurassic marine palynofloras are summarized here, based on the information from outcrop samples of 12 units, which were analyzed from a paleobiogeographic point of view. The configuration of the basin during the Early Jurassic was characterized mainly by partially interconnected depocenters, with restricted marine circulation that favored the development of associations dominated by components of the green lineage (acritarchs and prasinophytes). The Cuyo and Lotena groups (Middle Jurassic) were accumulated during two important flooding episodes which generated the paleoecological conditions for an increase in the diversity of the red lineage (dinocysts). Since the late Callovian the Hispanic Corridor connected the Neuquén Basin with the Tethyan realm allowing the free interchange of species. The Late Jurassic marine palynofloras are best characterized in the Vaca Muerta and Picún Leufú formations. The anoxic condition that prevailed during the accumulation of the Vaca Muerta Formation marked the return to the dominance of the green lineage. Conversely, the Picún Leufú Formation represents neritic more oxygenated bottom waters that favored a relative increase in the abundance and diversity of dinoflagellate cysts.

Key words. Jurassic. Marine palynofloras. Paleobiogeography. Neuquén Basin. Argentina.

Resumen. MICROPLANCTON MARINO DE PARED ORGÁNICA, JURÁSICO DE LA CUENCA NEUQUINA. DISTRIBUCIÓN, BIOESTRATIGRAFÍA Y PALEOBIOGEOGRAFÍA. UNA REVISIÓN. El Mesozoico constituye un momento crucial para analizar el recambio de los distintos linajes microplanctónicos producto del inicio de la ruptura de Pangea. La paleogeografía de Sudamérica y por lo tanto la de Argentina, experimentó sucesivos cambios durante este lapso de tiempo. La apertura de diferentes corredores oceánicos, principalmente durante el Jurásico, afectó los patrones de circulación global de los océanos, evidenciado en la Cuenca Neuquina en la variabilidad de composición de las asociaciones microplanctónicas de pared orgánica. Se reúne la información proveniente de muestras de afloramiento de 12 unidades jurásicas, cuyas palinofloras marinas fueron analizadas desde un punto de vista paleobiogeográfico. La configuración de la cuenca durante el Jurásico Temprano se caracterizó principalmente por la presencia de una serie de depocentros parcialmente interconectados con circulación marina restringida. Este contexto favoreció el desarrollo del linaje verde (acritarcos y prasinofíceas). Dos grandes episodios de inundación marina provocaron la acumulación de los grupos Cuyo y Lotena (Jurásico Medio) generando las condiciones paleoecológicas para un incremento en la diversidad del linaje rojo (dinoquistes). A partir del Caloviano tardío la apertura del Corredor Hispánico permitió la conexión de la Cuenca Neuquina con el Dominio Tethiano y con ello, el libre intercambio de especies. El Jurásico Tardío es aquí caracterizado por las palinofloras marinas de las formaciones Vaca Muerta y Picún Leufú. Las condiciones anóxicas que prevalecieron durante la acumulación de la Formación Vaca Muerta constituyen un retorno al predominio del linaje verde. Por el contrario, la Formación Picún Leufú caracterizada por ambientes de plataforma con aguas relativamente más oxigenadas, favorecieron el incremento en la abundancia y diversidad de dinoflagelados.

Palabras clave. Jurásico. Palinofloras marinas. Paleobiogeografía. Cuenca Neuquina. Argentina.

THE FOSSIL record of the Paleozoic–Mesozoic boundary documents one of the most dramatic changes in Phanerozoic marine primary production. It is generally agreed that acritarchs and prasinophytes essentially represent the marine phytoplankton of the Paleozoic Era (Riegel, 2008 and references therein). These groups were included by several authors (Falkowski *et al.*, 2005; Riegel, 2008 and references therein) in the "green lineage". Highly stratified anoxic bottom water overlain by low-salinity, warm surface waters were advantageous conditions for green algae (van de Schootbrugge *et al.*, 2005).

During the Middle–Late Triassic new groups of photosynthetic eukaryotic phytoplankton taxa, including cyst-forming dinoflagellates and calcareous nannoplankton (coccolithophorids), appeared (Riegel, 2008 and references therein), which represent the "red lineage" (Falkowski *et al.*, 2005 *in* van de Schootbrugge *et al.*, 2005). The radiation of cyst-forming dinoflagellates began in the Late Triassic showing a rapid increase during the Early Jurassic (Fensome *et al.*, 1996). This time was decisive for dinoflagellate evolution and during the late Pliensbachian they replaced green algae as primary producers. The break-up of Pangea played a crucial role in the spread of the red lineage (Katz *et al.*, 2004 in Riegel, 2008). The radiation of cyst-forming dinoflagellates during the late Sinemurian and late Pliensbachian coincided with significant changes in paleoceanography and paleoclimate, possibly related to the opening and flooding of the Hispanic Corridor (van de Schootbrugge *et al.*, 2005). Hydrographic instabilities and well-oxygenated bottom waters appear to have facilitated cyst-forming dinoflagellate diversity (Bucefalo Palliani *et al.*, 2002; van de Schootbrugge *et al.*, 2005; Sluijs *et al.*, 2005).

The main goal of this contribution is to describe the way these worldwide paleoceanographic changes affected the distribution and diversity patterns of organic-walled marine microplankton in the Neuquén Basin, Argentina, during the Jurassic.

GEOLOGICAL SETTING OF THE NEUQUÉN BASIN

The Neuquén Basin is situated in west-central Argentina and eastern Chile between 34° and 41°S (Fig. 1). This basin, originated during the latest Triassic, was an important region of sedimentation during the Jurassic and Early Cretaceous (Mpodozis and Ramos, 1989). It has been interpreted as a back-arc basin related to the thermal-tectonic collapse of the continental crust behind a stationary magmatic arc during the Late Triassic (Mpodozis and Ramos, 1989; Vergani *et al.*, 1995).

Permo-Triassic volcaniclastics, constituting the Choiyoi Group (Groeber, 1946; Stipanicic *et al.*, 1968) are regarded as basement. Deposits are mainly marine in origin and present well-defined records of cyclic sea-level changes at different scales (Howell *et al.*, 2005). The first major depositional episode after the basin was configured, the Cuyo Group (Groeber, 1946), comprises marine and continental deposits more than 2500 m thick, accumulated during a transgressive-regressive cycle which developed during the Hettangian–Middle Callovian (Zavala, 1996a). Although a Hettangian–Sinemurian marine transgression with ammonite fauna is recorded at the Río Atuel, Mendoza Province (Riccardi *et al.*, 1988), it did not reach the central and southern Neuquén Basin until the Pliensbachian. This group is composed of deposits consisting of a prograding clastic section with offshore fine-grained deposits of the Los Molles Formation (Weaver, 1931) (Fig. 2), isolated turbidite intervals and hyperpycnal flows (Zavala *et al.*, 2011, 2014; Martínez *et al.*, 2016). This formation is progressively overlain by sandstones and conglomerates reflecting shallow marine to continental environments belonging to the Lajas Formation (Weaver, 1931).

During the Early–Middle Jurassic the presence of a tectonic structure controlled the acumulation in the basin. This extensive and complex east-west oriented Mesozoic structure named Huincul Arch, located in the southern part of the Neuquén Basin, acted as a physical barrier isolating this part of the basin as a sub-basin named Picún Leufú (Hogg, 1993; Zavala and Freije, 2002). In this sub-basin the deposition of the Cuyo Group culminates with the continental deposits, red mudstones interbedded with sandstones and conglomerates, of the Challacó Formation (de Ferrariis, 1947; Zavala and González, 2001).

The Lotena Group (*sensu* Zavala and González, 2001) represents the second marine incursion after the first broad disconnection (Zavala, 2005). It is a clastic-evaporitic unit deposited during the middle Callovian until the latest Oxfordian–Early Kimmeridgian (Zavala 2005; Olivera *et al.*, 2010). This group starts with evaporites of the Tábanos Formation (Stipanicic, 1966; Dellapé *et al.*, 1979) followed by the Lotena Formation (*sensu* Gulisano *et al.*, 1984) (Fig. 2), which is dominated by mudstone with subordinate evaporites, limestones and sandstones. This unit is overlain by the mainly carbonate succession of the La Manga Formation (Stipanicic, 1966; Stipanicic *et al.*, 1975). The partial isolation of the Picún Leufú sub-basin continued during the be-

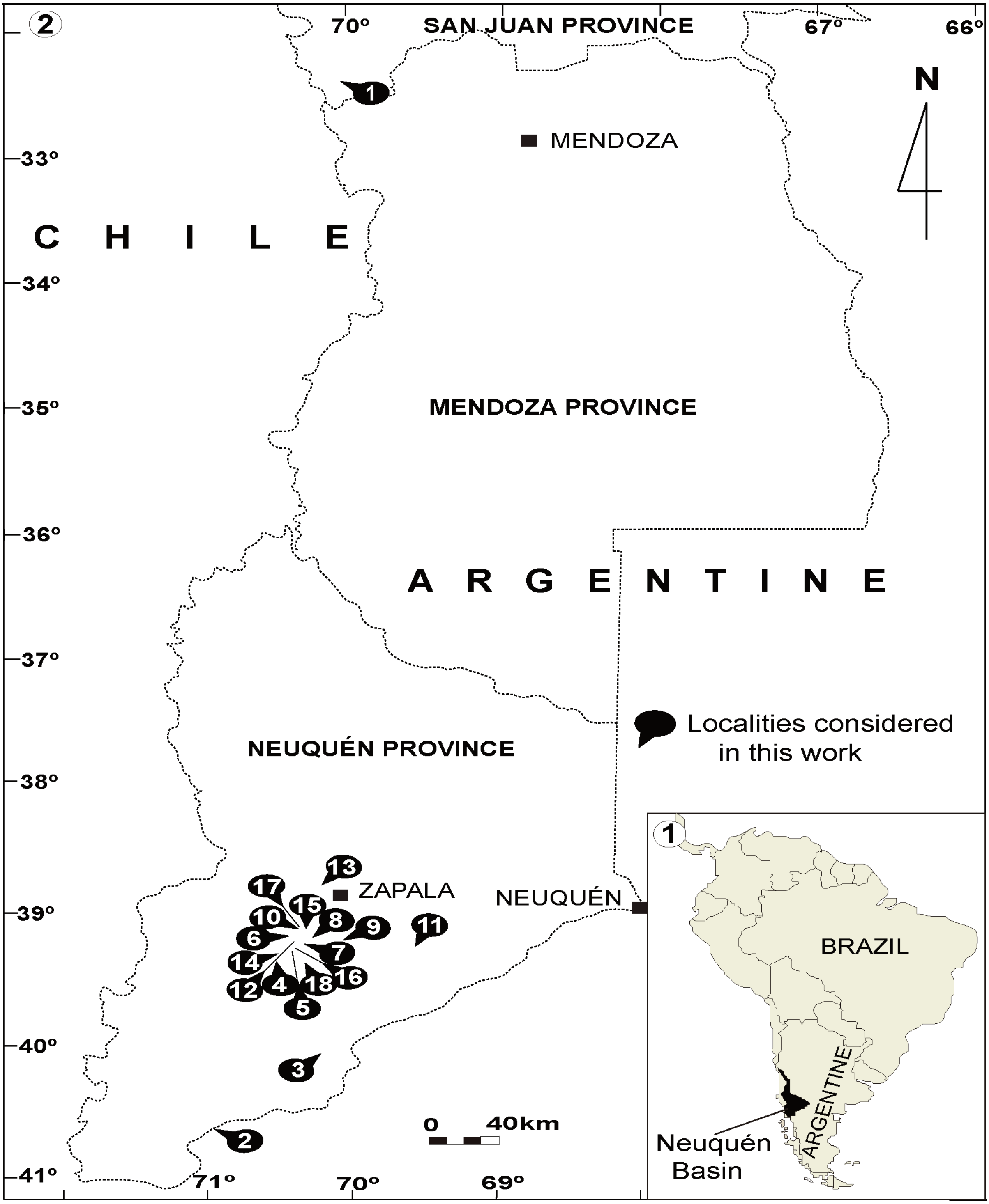


Figure 1. 1, Location map of the Neuquén Basin, Argentina, South America. **2,** Localities mentioned in the text; **1,** Arroyo de los Patos Sur (Los Patillos Fm.); **2,** Alicurá Dam (Nestares Fm.); **3,** Cañadón La Pintada (Piedra Pintada Fm.); **4,** Valle del Arroyo Lapa (Sierra Chacaico Fm.) and Arroyo Lapa-Estancia Charahuilla (Los Molles Fm.); **5,** Charauilla (Los Molles and Lajas formations); **6,** Puesto Bascuñán (Lajas Fm.); **7,** Puesto Policía (Los Molles Fm.); **8,** Los Molles (Los Molles and Lajas formations); **9,** Puente Picún Leufú (Los Molles, Lajas, Lotena, Vaca Muerta and Picún Leufú formations); **10,** Lohan Mahuida (Los Molles, Cura Niyeu and Lajas formations); **11,** Cerro Lotena (Los Molles Fm.); **12,** Cerro Chacaico (Los Molles and Lajas formations); **13,** Portada Covunco (Lajas, Lotena and Auquilco formations); **14,** Sierra Chacaico: Peregrina, Rhea Gorge, Quilmez and Dagna (Lajas Fm.); **15,** Quebrada del Sapo (Bosque Petrificado Fm.); **16,** Cura Niyeu (Cura Niyeu Fm.); **17,** Barda Norte (Lotena Fm.); **18,** Caichigüe (Vaca Muerta Fm.).

ginning of the accumulation of the Lotena Group. These deposits represent fluvial-lacustrine to estuarine enviroments and are known as the Bosque Petrificado Formation (Zavala and Freije, 2002), which is chronologically, but not genetically, related to the Tábanos Formation (Zavala and González, 2001; Zavala and Freije, 2002).

Marine sequences developed throughout the basin during the Late Jurassic–Early Cretaceous are included in the Mendoza Group (Stipanicic, 1969). This group comprises several units, the Auquilco (Weaver, 1931), Tordillo (Groeber, 1946; Stipanicic, 1966), Quebrada del Sapo (Digregorio, 1972), Vaca Muerta (Leanza and Hugo, 1978; Legarreta *et al.*, 1981; Veiga and Orchuela, 1988), Picún Leufú (Leanza 1973), Quintuco (Digregorio, 1972), Mulichinco (Digregorio, 1972) and Agrio (Weaver, 1931) formations widely extending from southern Neuquén to Mendoza provinces. The Auquilco Formation comprises an evaporitic succession of up to 400 m thick related to a marginal hypersaline marine environment (Legarreta and Uliana 1999; Volkheimer and Moroni 1981). The continental deposits of the Tordillo and Quebrada del Sapo formations represent a temporal isolation of the Neuquén Basin from the Pacific Ocean. During the Tithonian, catastrophic flooding represents the return to a depositional context of a marine basin with anoxic bottom water (Legarreta and Uliana, 1999), which corresponds to the deposits of the Vaca Muerta Formation. The top of this unit is diachronous and progradational. It includes younger stages when passing from the southern (middle Tithonian) to the central sector of the basin (Berriasian–Valanginian) (Doyle *et al.*, 2005). Near the southern border of the basin, the Vaca Muerta Formation is replaced laterally by the whitish and greenish calcareous sandstones, and massive whitish limestones of the Picún Leufú Formation.

All the units mentioned in this contribution are summarized in a correlation chart between two geological provinces, Principal Cordillera and Neuquén Embayment (Fig. 2).

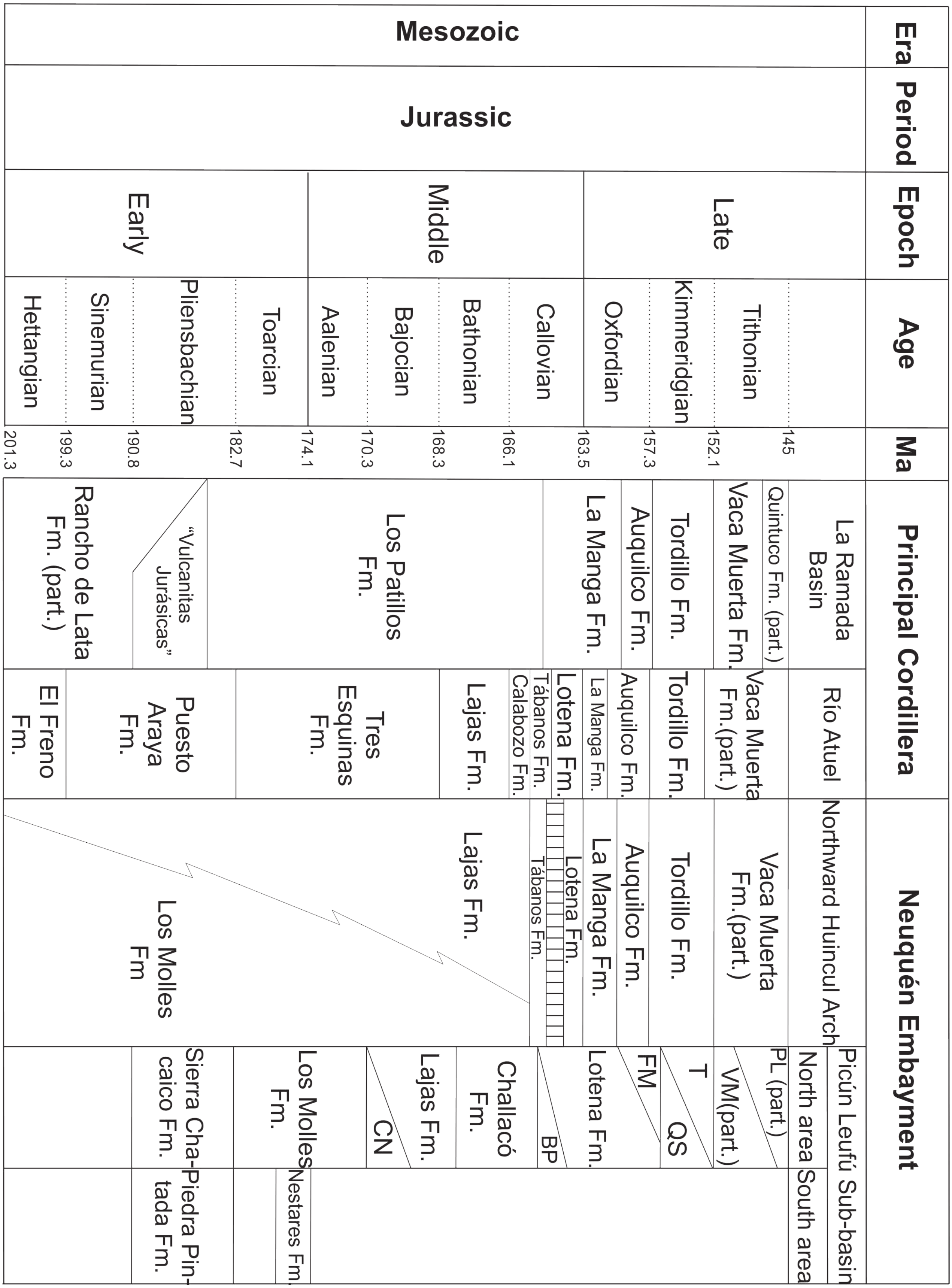
PALEOGEOGRAPHIC FRAMEWORK

The paleogeography of the beginning of the Jurassic was similar to the one of the end of the Paleozoic (Fig. 3). The supercontinent Pangea, surrounded by the superocean Panthalassa, represented a large barrier to the free movement of marine biotas along the paleo-equator. However, a system of rift valleys started to form within west-central Pangea since the latest Triassic (Iturralde-Vinent, 2006). In this area, Damborenea and Manceñido (1979) proposed the existence of a shallow intermittent marine connection between western Tethys and the eastern Pacific, based on bivalve data. This seaway, known as the Hispanic Corridor (Smith, 1983) acted as a filter which only allowed the interchange of on-shore benthonic species since the Sinemurian (Damborenea, 2000). The effective opening of this marine passage was installed during the Middle Jurassic. The stratigraphic record indicates that this connection was fully functional and the Circum-Tropical marine current was probably active since the Bathonian and certainly since the Oxfordian (Iturralde-Vinent, 2004, 2006).

By the late Pliensbachian another seaway, called the Viking Corridor by Westermann (1993), was opened between Greenland and Norway connecting the Arctic and Tethys oceans (Aberhan, 2001).

Another migration route was established during the Middle Jurassic (Bathonian and Callovian) with the opening of the Mozambique Corridor (Heinze, 1996; Abdelhady and Fürsich, 2015), which communicated Madagascar and

Figure 2. Correlation chart of selected Jurassic units from two geological provinces of Argentina. They are organized in integrated columns; only the main depocenters of these regions are taken into account, and they do not represent the entire units of each basin. The age range of each formation is mainly based on paleontological works (palynomorphs and ammonoids fossil-genera): La Ramada Basin: Volkheimer *et al.* (1977), Álvarez *et al.* (1994), Álvarez (1996); Río Atuel: Dimieri *et al.* (2005); Northward of Huincul Arch: Volkheimer and Moroni (1981), Zavala (1996 a,b), Martínez (2002), Martínez *et al.* (2005); Picún Leufú Sub-basin: Volkheimer (1973), Arguijo *et al.* (1982), González-Amicón and Volkheimer (1982a,b), Zavala and Freije (2002), Zavala *et al.* (2005), Armella *et al.* (2007), Zavattieri *et al.* (2008), Olivera *et al.* (2010). Abbreviations in the graphic: **CN**, Cura Niyeu Formation; **BP,** Bosque Petrificado Formation; **FM,** Fortín Primero de Mayo Formation; **QS,** Quebrada del Sapo Formation; **T,** Tordillo Formation; **VM (part.),** Vaca Muerta Formation (partially); **PL (part.),** Picún Leufú Formation (partially).


Era
Period
Epoch
Age
Ma
Mesozoic
Jurassic
Early
Middle
Late
Hettangian
Sinemurian
Pliensbachian
Toarcian
Aalenian
Bajocian
Bathonian
Callovian
Oxfordian
Kimmeridgian
Tithonian
201.3
199.3
190.8
182.7
174.1
170.3
168.3
166.1
163.5
157.3
152.1
145
Principal Cordillera
La Ramada Basin
Quintuco Fm. (part.)
Vaca Muerta Fm.
Tordillo Fm.
Auquilco Fm.
La Manga Fm.
Los Patillos Fm.
"Vulcanitas Jurásicas"
Rancho de Lata Fm. (part.)
Río Atuel
Vaca Muerta Fm.(part.)
Tordillo Fm.
Auquilco Fm.
La Manga Fm.
Lotena Fm.
Tábanos Fm.
Calabozo Fm.
Lajas Fm.
Tres Esquinas Fm.
Puesto Araya Fm.
El Freno Fm.
Neuquén Embayment
Northward Huincul Arch
Vaca Muerta Fm.(part.)
Tordillo Fm.
Auquilco Fm.
La Manga Fm.
Lotena Fm.
Tábanos Fm.
Lajas Fm.
Los Molles Fm
Picún Leufú Sub-basin
North area
South area
PL (part.)
VM(part.)
T
QS
FM
Lotena Fm.
BP
Challacó Fm.
Lajas Fm.
CN
Los Molles Fm.
Nestares Fm.
Sierra Chacaico Fm.
Piedra Pintada Fm.

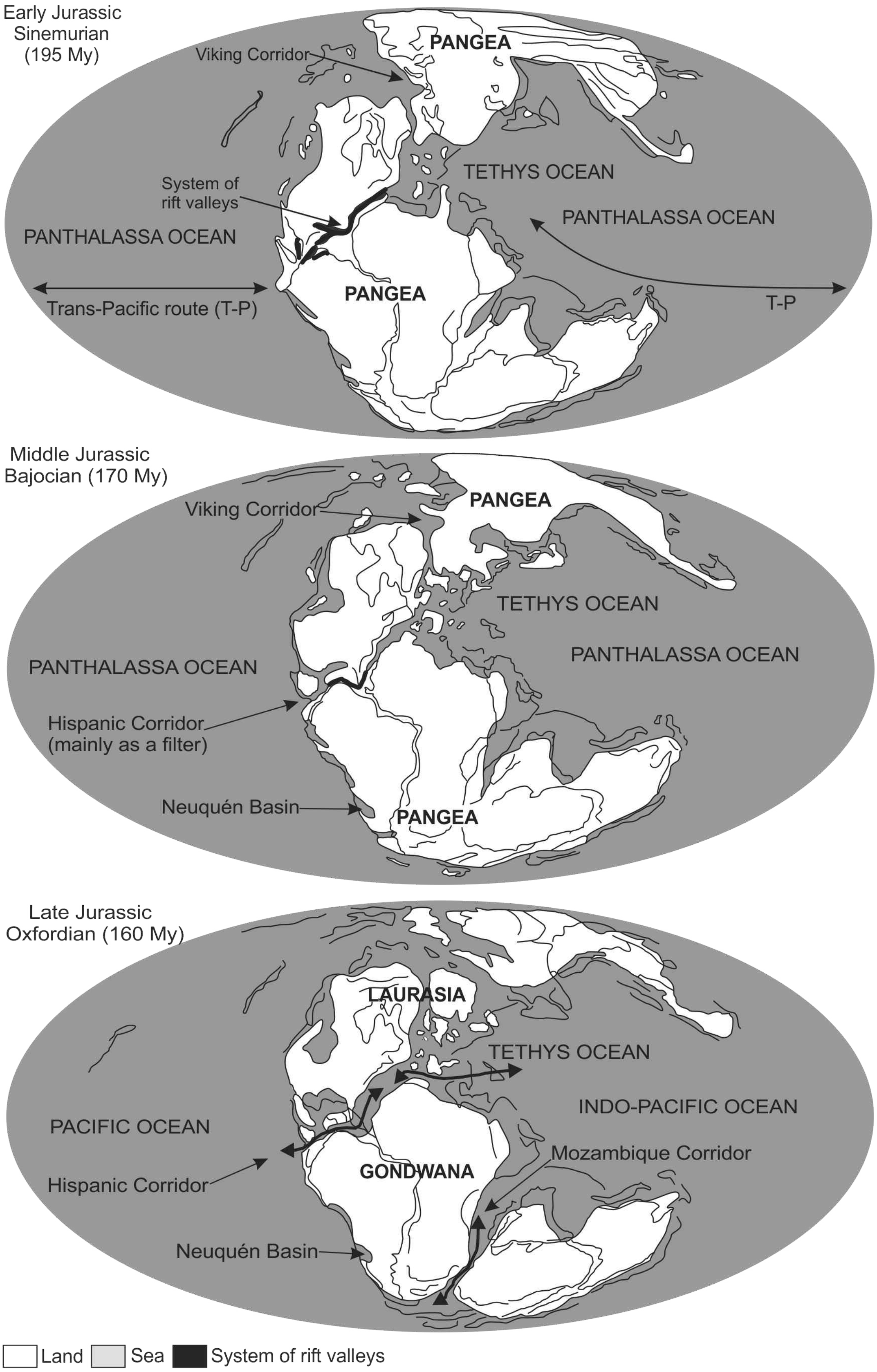


Figure 3. Paleogeographic maps of the Jurassic world (modified from Iturralde-Vinent, 2006).

southern Africa with the South Pacific. This seaway became wider towards the Oxfordian, allowing the incoming of the high-latitude bivalve taxa into the East African (Damborenea *et al*., 2013).

DISTRIBUTION OF ORGANIC-WALLED MARINE MICROPLANKTON FROM THE NEUQUÉN BASIN

The deposits of the Neuquén Basin are characterized by alternating transgressive marine and regressive non-marine phases. Thus, the stratigraphical record of marine organic-walled microplankton (dinoflagellates, prasinophytes, acritarchs and other algae) is discontinuous (Tab. 1). However, the distribution of mainly dinoflagellate cysts enabled an outline of general paleobiogeographic patterns. The Neuquén Basin has a significantly refined biozonation in terms of resolution based on abundant, diverse and very well preserved ammonite faunas. In this paper, the word "diversity" is used in its original sense to denote the number of species (Rosenzweig, 1995). Riccardi (2008) presented an update of these zonations.

Early Jurassic

Currently, only five Liassic formations of the Neuquén Basin have provided palynological assemblages: Los Patillos (Álvarez *et al*., 1994), Piedra Pintada (Stipanicic *et al*., 1968; Gulisano and Pando, 1981), Sierra Chacaico (Volkheimer, 1973), Los Molles (Weaver, 1931) and Nestares (González Díaz, in Arrondo and Petriella, 1980) (Figs. 1, 2; Tabs. 1, 2).

Volkheimer *et al*. (1978) studied the lower (continental) and upper (marine) Member of the Los Patos Formation in the northern part of the Neuquén Basin (western slope of Espinacito Range, High Cordillera of San Juan). The upper Member contains ammonites of the *Fanninoceras* Assemblage Zone (see Riccardi *et al*., 1990, 2000) (late Pliensbachian) and *Tenuicostatum* Standard Zone and *Dactylioceras hoelderi* Assemblage Zone (see Riccardi, 2008) (early Toarcian). The marine elements are represented only by acritarchs (*Schizocystia rara* Playford and Dettman 1965, *Leiosphaeridia* sp.) and prasinophytes (*Pleurozonaria* sp., *Cymatiosphaera* sp.). After Álvarez *et al*. (1994) the original Los Patos Formation should be considered a *nomen nudum*. They proposed that Los Patos should be divided in two units: Rancho de Lata and Los Patillos formations. The levels studied by Volkheimer *et al*., (1978), under the name upper Member, should now be considered as belonging to the lower section of Los Patillos Formation (Fig. 2).

A marine sequence, belonging to the Piedra Pintada Formation, crops out near Piedra del Aguila (southern border of the Neuquén Basin), which was assigned to the Pliensbachian due to the presence of *Austromorphites behrendseni* Jaworski (Arguijo *et al*., 1982; Arguijo and Volkheimer, 1985). The marine components of the recovered palynological association are represented by cf. *Granodiscus staplinii* (Pocock) Jiabo 1978, *Tasmanites suevicus* (Eisenack) Wall 1965 and proximate indeterminate dinocysts. The Sierra Chacaico and Los Molles formations from the Sierra de Chacaico area yielded guide ammonites of the *Austromorphites behrendseni* Assemblage Zone (Hillebrandt, 1987, 2006) (late early Pliensbachian) and *Dactylioceras hoelderi* Assemblage Zone (see Hillebrandt, 1987; Riccardi *et al*., 1990, 2000; Hillebrandt *et al*., 1992) (early Toarcian), respectively (Volkheimer, 1973). The recovered marine palynological assemblages from these units are characterized by acritarchs (*Solisphaeridium* cf. *debilispinum* (Wall and Downie) Sarjeant 1973 and *Micrhystridium* sp.) and prasinophytes (*Campenia austroamericana* Volkheimer 1974, *Lancettopsis* sp., *Pterospermopsis* sp. A, *Pterospermopsis* sp. B and *Tasmanites suevicus*) (Volkheimer, 1974).

An Early Jurassic siliciclastic sequence crops out at Alicurá (Limay River) in the southern part of the Neuquén Basin. The marine assemblage recovered from the Las Coloradas Formation (Quartino *et al*., 1981) was studied by Volkheimer *et al*. (1981), and assigned to the Pliensbachian–early Toarcian age. This unit is characterized by acritarchs, *Hyalinsphaeridia* cf. *hyalina* (Deflandre) Bernier and Courtinat 1979, *G. staplinii*), *Deunffia* and *Leiofusa.* Zavattieri *et al*. (2008) discussed the stratigraphic position of this unit, which for priority reasons is called the Nestares Formation (Fig. 2). These authors presented an interesting assemblage characterized by marine components, such as the *Parvocysta* suite, *Phallocysta*, *Nannoceratopsis* and Suessiaceae (Figs. 5.15-16) and *Callialasporites trilobatus* (Balme) Dev 1961 pollen grains, among others, based on a new sampling at the Alicurá Dam. This palynoflora suggests a late Toarcian age; therefore they relocated this unit to the basal part of the Cuyo Group.

Table 1 - Distribution of Jurassic organic-walled marine microplankton species from Neuquén Basin.

		Taxa	*Formations*											
			Los Patillos	*Piedra Pintada*	*Sierra Chacaico*	*Nestares*	*Los Molles*	*Cura Niyeu*	*Lajas*	*Bosque Petrificado*	*Lotena*	*Auquilco*	*Vaca Muerta*	*Picún Leufú*
Green lineage	*Prasinophytes*	**Cymatiosphaera** *spp.*	X			X	X	X	X		X		X	
		Pleurozonaria *spp.*	X				X	X						
		Tasmanites suevicus *(Eisenack) Wall 1965*		X			X							
		Campenia austroamericana *Volkheimer 1974*			X		X							
		Lancettopsis *sp. (in Volkheimer 1974)*			X		X	X						
		Pterospermopsis *sp. A (in Volkheimer 1974)*			X									
		Pterospermopsis *sp. B (in Volkheimer 1974)*			X									
		Cymatiosphaera eupeplos *(Valensi) Deflandre 1954*					X		X		X		X	
		Cymatiosphaera *cf.* **C. eupeplos** *(in Martínez* et al. *2005)*					X							
		Cymatiosphaera *cf.* **C. volkheimerii** *(in Martínez* et al. *2005)*					X							
		Cymatiosphaera *sp. 1 (in Martínez* et al. *2005)*					X							
		Cymatiosphaera *sp. 2 (in Martínez* et al. *2005)*					X							
		Cymatiosphaera *sp. 3 (in Martínez* et al. *2005)*					X							
		Pleurozonaria *cf.* ***P.*** **picunensis** *(in Martínez* et al. *2005)*					X							
		Tasmanites *spp.*					X		X					
		Campenia *sp.*						X						
		Pleurozonaria picunenesis *Quattrocchio 1980*							X				X	X
		Pterosphaeridia *spp.*							X		X			
		Cymatiosphaera volkheimerii *(Quattrocchio) Martínez* et al. *2005*											X	X
		Pterospermella hartii *(Sarjeant) Eisenack* et al. *1973*											X	
	Acritarchs	**Schizocystia** *sp. cf.* **S. rara** *(in Volkheimer* et al. *1978)*	X											
		Leiosphaeridia *spp.*	X			X		X	X		X			X
		Solisphaeridium *cf.* **debilispinum** *(in Volkheimer* et al. *1974)*			X			X						
		Deunffia *sp.*				X								
		Leiofusa *sp.*				X								
		Hyalinsphaeridia *sp. cf.* **H. hyalina** *(in Quattrocchio 1980)*				X	X		X		X	X		
		Granodiscus staplinii *(Pocock) Jiabo 1978*				X								
		Micrhystridium *spp.*				X	X	X	X	X	X		X	
		Schizocystia *sp.*				X								
		Veryhachium *spp.*				X		X			X			
		Baltisphaeridium *spp.*					X				X			
		Comasphaeridium *cf.* **debilispinum**					X							
		Filisphaeridium balmei *(Sarjeant) Sarjeant and Stancliffe 1994*					X				X			
		Filisphaeridium *cf.* **F. balmei** *(in Martínez* et al. *2005)*					X							
		Filisphaeridium castaninum *(Valensi) Sarjeant and Stancliffe 1994*					X							
		Filisphaeridium densispinum *(Valensi) Sarjeant and Stancliffe 1994*					X							
		Leiosphaeridia *sp. B (in Volkheimer* et al. *1977)*					X				X			
		Leiosphaeridia *sp. E (in Prámparo 1989)*					X							
		Leiosphaeridia *cf.* **L.** *sp. F (in Martínez* et al. *2005)*					X							

Table 1 - Continuation.

		Taxa	*Formations*											
			Los Patillos	*Piedra Pintada*	*Sierra Chacaico*	*Nestares*	*Los Molles*	*Cura Niyeu*	*Lajas*	*Bosque Petrificado*	*Lotena*	*Auquilco*	*Vaca Muerta*	*Picún Leufú*
Green lineage	*Acritarchs*	**Micrhystridium fragile** *Deflandre 1947*					X		X		X			
		M. echinoides *cf. forma* **minor** *(in Martínez* et al*. 2005)*					X							
		M. brevispinosum *(Valensi) Sarjeant and Stancliffe 1994*					X		X		X			
		Micrhystridium *cf.* **M. gregarium** *(in Martínez* et al*. 2005)*					X							
		M. inconspicuum *(Deflandre)* emend. *Deflandre and Sarjeant 1970*					X		X		X		X	
		Micrhystridium *cf.* **M. inconspicuum** *(in Martínez* et al*. 2005)*					X							
		Micrhystridium nannacanthum *Deflandre 1945*					X		X	X				
		Micrhystridium recurvatum *Valensi 1953*					X		X		X		X	
		Polygonium *sp. cf. ?***P. jurassicum** *(in Martínez* et al*. 2005)*					X							
		Polygonium *spp.*					X		X		X			
		Veryhachium valensii *(Valensi) Downie and Sarjeant 1965*					X							
		Hyalinsphaeridia hyalina *(Deflandre) Bernier and Courtinat 1979*						X			X		X	
		Granodiscus *sp. cf.* **G. staplinii** *(in Quattrocchio 1984a)*						X			X		X	X
		Deunffia monospinosa *Downie 1960*							X					
		Leiosphaeridia *sp. C (in Quattrocchio and Volkheimer 1983)*							X		X			
		Leiosphaeridia *cf.* **L.** *sp. B (in Volkheimer* et al*. 1977)*							X		X			
		Micrhystridium echinoides *Valensi 1953*							X		X			
		Micrhystridium placophorum *Valensi 1948*							X					
		M. recurvatum *forma* **recurvatum** *Valensi 1953*							X		X			
		Micrhystridium stellatum *Deflandre 1945*							X					
		Solisphaericium stimuliferum *(Deflandre) Pocock 1972*								X				X
		Hyalinsphaeridia acorpuscula *Bernier and Courtinat 1979*									X			
		G. *sp. cf.* **G. granulatus** (*in Volkheimer and Quattrochio 1981*)									X			
		Micrhystridium rarispinum *Sarjeant 1960*									X			
		Granodiscus granulatus *Mädler 1963*										X		
		Leiosphaeridia *sp. cf.* **L. variabilis**										X		
		Comasphaeridium *sp.*											X	
		Filisphaeridium *sp.*											X	
		Hyalosphaera *sp.*											X	
		Leiosphaeridia *sp. A (in Volkheimer and Quattrocchio 1977)*											X	
		Lecithodinium *sp.*												X
		Micrhystridium lymensis *var.* **gliscum** *Wall 1965*												X
Red lineage	*Dinoflagellate cysts*	**Batiacasphaera** *sp.*				X								
		Mancodinium *sp.*				X								
		Mendicodinium *sp.*				X								
		Nannoceratopsis *spp.*				X		X	X					
		Phallocysta *spp.*				X								
		Parvocysta *sp.*				X								
		Sentusidinium *sp.*				X								

TABLE 1 - Continuation.

		Taxa	Formations											
			Los Patillos	*Piedra Pintada*	*Sierra Chacaico*	*Nestares*	*Los Molles*	*Cura Niyeu*	*Lajas*	*Bosque Petrificado*	*Lotena*	*Auquilco*	*Vaca Muerta*	*Picún Leufú*
Red lineage	*Dinoflagellate cysts*	**Parvocysta** *sp.*				X								
		Sentusidinium *sp.*				X								
		Cleistosphaeridium sp.					X							
		Escharisphaeridia pocockii (*Sarjeant*) *Erkmen and Sarjeant 1980*					X		X	X			X	X
		Gonyaulacysta *spp.*						X			X			X
		Pareodinia *sp. A (in Quattrrocchio 1984a)*						X						
		Rhaetogonyaulacaceae *Tipo 1 (in Quattrrocchio 1984a)*						X						
		Rhaetogonyaulacaceae *Tipo 2 (in Quattrrocchio 1984a)*						X						
		Rhaetogonyaulax *sp.*						X						
		Acanthaulax *sp.*							X					
		Ctenidodinium *spp.*							X		X			X
		Dissiliodinium psilatum *Prauss 1989*							X					
		Dissiliodinium *cf.* **baileyi** *(in Stukins* et al. *2013)*							X					
		Dissiliodinium *spp.*							X					
		Endoscrinium *spp.*							X		X			
		Escharisphaeridia *spp.*							X					
		Jansonia psilata *Martínez* et al. *1999*							X				X	
		Kallosphaeridium granulatum *(Norvick) Stover and Evitt 1978*							X					
		Kallosphaeridium *spp.*							X					
		Korystocysta kettonensis *(Sarjeant) Woollam 1983*							X					
		Korystocysta *sp.*							X					
		Mendicodinium groenlandicum *(Pocock and Sarjeant) Davey 1979*							X		X			
		Nannoceratopsis pellucida *Deflandre* emend. *Evitt 1961*							X		X			
		Rhynchodiniopsis cladophora *(Deflandre) Below 1981*							X		X			
		Acanthaulax downiei *(Sarjeant) Sarjeant 1976*									X		X	
		Ambonosphaera*?***Staffinensis** *(Gitmez) Poulsen and Riding 1992*									X			
		Barbatacysta *cf.* **brevispinosa** *(in Courtinat and Gaillard 1980)*									X			
		Chytroeisphaeridia chytroeides *(Sarjeant) Downie and Sarjeant 1965*									X			
		Cleistosphaeridium lumectum *(Sarjeant) Davey* et al. *1969*									X			
		Diacanthum argentinum *Quattrocchio and Sarjeant 1992*									X			X
		Dissiliodinium volkheimeri *Quattrocchio and Sarjeant 1992*									X			
		Durotrigia *sp.*									X			
		Ellipsoidictyum gochtii *Fensome 1979*									X			
		Endoscrinium galeritum *subsp.* **reticulatum** *Klement 1960*									X			
		E. *cf.* **E. g. subsp. reticulatum** *(in Riding* et al. *2011)*									X			
		Gonyaulacysta jurassica *(Deflandre) Norris and Sarjeant 1965*									X		X	
		Gonyaulacysta jurassica *subsp.* **adecta** *(Deflandre) Sarjeant 1982*									X			
		Hystrichosphaeridium *sp. A (in Volkheimer and Quattrochio 1981*)									X			
		Liesbergia liesbergensis *Berger 1986*									X			

TABLE 1 - Continuation.

		Taxa	*Formations*											
			Los Patillos	*Piedra Pintada*	*Sierra Chacaico*	*Nestares*	*Los Molles*	*Cura Niyeu*	*Lajas*	*Bosque Petrificado*	*Lotena*	*Auquilco*	*Vaca Muerta*	*Picún Leufú*
Red lineage	*Dinoflagellate cysts*	**Limbodinium absidatum** *(Drugg) Riding 1987*									X			
		Lithodinia deflandrei *Sarjeant 1968*									X			
		Lithodinia jurassica *subsp.* **reburrosa** *(Eisenack* emend. *Gocht 1975) Quattrocchio and Sarjeant 1992*									X			
		Lithodinia *spp.*									X			
		Mancodinium semitabulatum *Morgenroth 1970*									X			
		Rhynchodiniopsis *spp.*									X			
		Sentusidinium villersense *(Sarjeant) Sarjeant and Stover 1978*									X			X
		Scriniocassis weberi *Gocht 1962*									X			
		Scriniodinium crystallinum *(Deflandre) Klement 1960*									X			
		Trichodinium scarburghensis *(Sarjeant) Williams* et al. *1993*									X			
		Tubotuberella dangeardii *(Sarjeant) Stover and Evitt 1978*									X			
		Pareodinia *sp.*									X			X
		Pareodinia ceratophora *var.* **pachyceras** *Sarjeant 1959*									X		X	
		Pareodinia ceratophora *Deflandre 1947*									X		X	
		Protobatioladinium *cf.* **P. lindiensis** *(in Riding* et al. *2011)*									X			
		Wanaea acollaris *Dodekova 1975*									X			
		Acanthaulax *aff.* **Paliuros** *(Sarjeant) Sarjeant 1968*											X	
		Apteodinium bucculiatum *Davies 1983*											X	
		Dichadogonyaulax *cf.* **schizoblata** *(in Quattrocchio and Sarjeant 1992)*											X	
		Hystrichosphaerina neuquina *(Quattrocchio and Volkheimer) emend. Quattrocchio and Sarjeant 1992*											X	X
		Kalyptea diceras *Cookson and Eisenack 1960*											X	
		Microdinium *sp. A (in Vokheimer and Quattrocchio 1977)*											X	
		Paraevansia *sp.*											X	X
		Aptea notialis *Quattrocchio and Sarjeant 1992*												X
		Cribroperidinium *sp.*												X
		Ctenidodinium tenellum *Deflandre 1938*												X
		Diacanthum *cf.* **hollisteri** *(in Quattrocchio and Sarjeant 1992)*												X
		Dichadogonyaulax culmula *subsp.* **curtospina** *(Norris) Quattrocchio and Sarjeant 1992*												X
		Dingodinium *sp.*												X
		Millioudodinium nuciforme *(Deflandre) Sarjeant 1982*												X
		Paraevansia mammillata *Quattrocchio and Sarjeant 1992*												X
		Pilosidinium cactosum *Quattrocchio and Sarjeant 1992*												X
		Rhynchodiniopsis setcheyensis *(Sarjeant) Sarjeant 1982*												X
		Rhynchodiniopsis *cf.* **setcheyensis** *(in Quattrocchio and Sarjeant 1992)*												X
		Systematophora penicillata *(Ehrenberg)* emend. *Sarjeant 1980*												X

Table 2 - Middle Jurassic localities considered in this study (the age of the units is based on paleontological contributions, main ammonoids and palynomorphs data, carried out by different authors and it does not represent the entire age range of each unit).

Formation	Age	Localities	Contributions
Picún Leufú	late middle Tithonian–early Berriasian	Picún Leufú Creek	17
Vaca Muerta (partially)	early–middle Tithonian early Tithonian	PPL Caichigüe	14, 17, 18, 26, 27
Auquilco	late Oxfordian	PC	25
Lotena	late Callovian middle–late Callovian	Portada Covunco (PC) Puente Picún Leufú (PPL)	9, 19 17, 19, 28
Bosque Petrificado	Callovian	Quebrada del Sapo	12
Lajas	Middle Jurassic	M, Ch Sierra de Chacaico	5, 20 21, 22, 23
	late Aalenian/early Bajocian–early Callovian	LM, PPL, PC, Puesto Bascuñán, CC	3, 4, 8, 10, 11
Cura Niyeu	early–middle Bajocian	LM Cura Niyeu	15, 16 6, 7
Los Molles	early Bajocian	Charahuilla (Ch)	5
	late Aalenian–early Bajocian	Lohan Mahuida (LM), Los Molles (M), Co. Lotena, PPL, Puesto Policía, Co. Chacaico (CC)	3, 8, 12, 13
	early Toarcian	Sierra de Chacaico	24
Nestares	late Toarcian	Alicurá Dam	30, 31
Sierra Chacaico	late Early Pliensbachian	Sierra de Chacaico	24
Piedra Pintada	Pliensbachian	Piedra del Aguila	1, 2
Los Patillos	late Pliensbachian–early Toarcian	Arroyo de Los Patillos	29

1, Arguijo and Volkheimer, (1985); 2, Arguijo et al. *(1982); 3, García, (1998); 4, García* et al. *(1994); 5, García* et al. *(2006); 6, González-Amicón and Volkheimer, (1982a); 7, González-Amicón and Volkheimer, (1982b); 8, Martínez, (1999); 9, Martínez and Quattrocchio, (2004); 10, Martínez* et al. *(1999); 11, Martínez* et al. *(2001); 12, Martínez* et al, *(2005); 13, Martínez* et al. *(2008); 14, Quattrocchio, (1980); 15, Quattrocchio, (1984a); 16, Quattrocchio, (1984b); 17, Quattrocchio and Sarjeant, (1992); 18, Quattrocchio and Volkheimer, (1990); 19, Riding* et al. *(2011); 20, Scafati and Morbelli, (1984); 21, Stukins, (2011); 22, Stukins* et al. *(2013a); 23, Stukins* et al. *(2013b); 24, Volkheimer, (1973); 25, Volkheimer and Moroni, (1981); 26, Volkheimer and Quattrocchio, (1975) ; 27, Volkheimer and Quattrocchio, (1977); 28, Volkheimer and Quattrocchio, (1981); 29, Volkheimer* et al. *(1978); 30, Volkheimer* et al. *(1981); 31, Zavattieri* et al. *(2008).*

As pointed out above, during Early Jurassic times the organic-walled marine microplankton assemblages were very scarce and of low diversity in the Neuquén Basin. Mainly acritarchs and prasinophytes have been identified. The first diversified dinoflagellate cyst recorded in the South American late Early Jurassic was found in the late Toarcian Nestares Formation (Zavattieri *et al.*, 2008).

Middle Jurassic

The palynology of Middle Jurassic deposits of the Neuquén Basin has been widely studied during the last five decades. Several formations have provided well preserved continental and marine palynofloras (Figs. 1, 2; Tabs. 1–2). The Middle Jurassic units of the Cuyo Group represent the first effective oceanic incursion into the Neuquén Embayment. These paleoenvironmental conditions led to more relatively abundant and diversified microplanktonic marine assemblages than the Liassic associations. The majority of the analyzed formations represent marginal marine environments, yielding marine assemblages mainly dominated by acritarchs (*Micrhystridium* and *Veryhachium* complexes) and prasinophytes (*e.g.*, *Cymatiosphaera*, *Pleurozonaria* and *Tasmanites*).

The Los Molles Formation, in west-central Argentina, was carefully calibrated through the ammonite zonation. Zavala (1996b) reported the presence of ammonite fauna belonging to the *Malarguensis* Standard Zone, *Singularis* Standard Zone, and *Giebeli* Standard Zone, which suggests a late Aalenian–early Bajocian age. The marine components of the palynoflora from this formation are characterized by acritarchs (mainly Acanthomorphitae) and prasinophytes; dinocysts are scarce, *Escharisphaeridia pocockii* (Sarjeant) Erkmen and Sarjeant, 1980 (Fig. 5.19) and *Cleistosphaeridium* sp. These assemblages are in agreement with a marginal-marine environment with sub-normal salinity (Martínez *et al.*, 2008).

The stratigraphic position of the Lajas Formation is given by ammonite data. The presence of *Singularis* Standard Zone, *Giebeli* Standard Zone, *Humphriesianum* Standard Chronozone, *Rotundum* Standard Chronozone, and *Vergarensis* Standard Zone suggests an early Bajocian–early Callovian age (Zavala, 1996b, Quattrocchio *et al.*, 2007). This coincides with the age proposed by Stukins *et al.* (2013a), based on dinoflagellate cyst assemblages. The Lajas dinocyst assemblages are scarce, predominating proximate forms (*Escharisphaeridia pocockii*), species indicative of euhryaline conditions (*Nannoceratopsis pellucida* Deflandre *emend.* Evitt, 1961) and opportunistic taxa, *Jansonia psilata* Martínez *et al.*, 1999 (Figs. 5.17–18), (Martínez *et al.*, 1999; Martínez and Quattrocchio, 2005). Stukins (2011) and Stukins *et al.* (2013a,b) reported an early Bajocian assemblage containing *Dissiliodinium psilatum* Prauss 1989 and *Korystocysta kettonensis* (Sarjeant) Woollam 1983 at Sierra de Chacaico. In the uppermost part of the Lajas Formation, in Portada Covunco, these authors mentioned the presence of *Rhynchodiniopsis cladophora* (Deflandre) Below 1981 in association with *Mendicodinium groenlandicum* (Pocock and Sarjeant) Davey 1979 suggesting an early Callovian age.

Cura Niyeu (at Lohan Mahuida) and Lotena formations yielded diversified and abundant dinocyst assemblages. The Cura Niyeu Formation contains ammonite faunas including lower Bajocian *Sonninia* cf. *zitteli* and *S. espinazitensis* and middle Bajocian *Chondroceras submicrostomum* and *Otoites* sp. (Quattrocchio, 1984a). The marine assemblage is mainly composed of acavate forms, such as rhaetogonyaulacoid cysts and *Nannoceratopsis* species (Quattrocchio and Volkheimer, 1990) (Tab. 1).

Lotena palynological marine associations have been recovered from Puente Picún Leufú and Portada Covunco (Quattrocchio and Sarjeant, 1992; Martínez and Quattrocchio, 2004). These sediments are considered as mid–late Callovian in age (Groeber *et al.*, 1953; Stipanicic, 1969; Riccardi *et al.*, 1990; Riccardi 2008) on account of the ammonite identified in the former locality, *Rehmannia* (*Loczyceras*) *patagoniensis* (Dellapé *et al.*, 1979). The Lotena Formation at the Portada Covunco section lacks ammonite faunas, however the underlying Lajas Formation yielded *Eurycephalites* cf. *vergarensis*, which is characteristic of the *Vergarensis* Chronozone, and suggests an early Callovian age (Riccardi *et al.*, 1989, 1990; Riccardi, 2008). The organic-walled marine microplankton of this unit is characterized by the appearance of chorate cysts (Quattrocchio and Volkheimer, 1990; Quattrocchio and Sarjeant, 1992). Riding *et al.* (2011) restudied the palynological samples of the localities mentioned above, and refined the biostratigraphy based on the dinocyst assemblages. These authors suggested a late Callovian age taking into account the first appearance of *Limbodinium absidatum* (Drugg) Riding 1987, *Wanaea acollaris* Dodekova 1975, and *Scriniodinium crystallinum* (Deflandre) Klement 1960.

The Bosque Petrificado Formation (Zavala and Freije, 2002= "Challacó" Formation of Zavala and González, 2001) lacks ammonite control; however, it has been correlated with the basal part of the Lotena Formation. Thus, a Callovian age was suggested for these strata (Zavala and Freije, 2002), which was later confirmed by palynological studies (Martínez *et al.*, 2005). At the Quebrada del Sapo section this unit yielded a marginal marine assemblage characterized by *Escharisphaeridia pocockii* and *Micrhystridium* complex (Martínez *et al.*, 2005).

Late Jurassic

Four units provided well preserved continental and marine palynofloras: Lotena, Auquilco, Vaca Muerta and Picún Leufú formations. However, the most diversified dinocyst assemblages were found in the Vaca Muerta and Picún Leufú formations (Figs. 1, 2; Tabs. 1–2).

Olivera *et al.* (2010) suggested marginal marine conditions at least until the latest Oxfordian–early Kimmeridgian for the Lotena Formation at Picún Leufú sub-basin (Barda

Norte locality), based on the presence of organic-walled marine microplankton and foraminifers.

The Auquilco Formation at Portada Covunco, late Oxfordian in age (Volkheimer and Moroni, 1981) bears a well preserved palynoflora deposited in a near shore marine environment. The microplankton is scarce and of low diversity, exclusively represented by acritarchs Sphaeromorphitae (*G. granulatus*, *Leiosphaeridia* sp. cf. *L. variabilis, Hyalinsphaeridia* cf. *hyalina*) and Acanthomorphitae (cf. *Baltisphaeridium* sp.).

The Vaca Muerta Formation has already been studied palynologically at Caichigüe and Puente Picún Leufú (Volkheimer and Quattrocchio, 1975, 1977; Quattrocchio, 1980; Quattrocchio and Volkheimer, 1990; Quattrocchio and Sarjeant, 1992). Fragmentary ammonites assigned to *Virgatosphinctes* sp. found in the Caichigüe area, together with correlation with the fossiliferous beds of the near locality of Charahuilla, suggest an early Tithonian age (Volkheimer and Quattrocchio, 1975). The marine association recovered from these sediments is widely dominated by acritarchs and prasinophytes, whereas dinocysts are very scarce (Volkheimer and Quattrocchio, 1977).

The lower part of the Vaca Muerta Formation sequence at Puente Picún Leufú yielded ammonites, including *Choicensisphinctes choicensis* (Burckhardt) and *Torquatisphinctes* sp. belonging to the *Virgatosphinctes mendozanus* Zone (Burckhardt 1900) of the latest early to middle Tithonian (Riccardi, 2008). This formation includes younger strata towards the centre of the Neuquén Basin (Leanza *in* Quattrocchio and Sarjeant, 1992). The organic-walled marine microplankton from the middle part of the Vaca Muerta Formation at the Puente Picún Leufú section shows similar proportions of dinocysts and acritarchs/prasinophytes suggesting a shallow marine environment (Quattrocchio and Sarjeant, 1992).

At the southeastern margin of the basin, the Vaca Muerta Formation is overlain by the shallow marine carbonates and siliciclastic sediments of the Picún Leufú Formation. A few ammonite levels yielding *Subdichotomoceras*, *Lytohoplites*, *Corongoceras* and *Substeueroceras* in the type locality, Picún Leufú Creek, suggest these sediments range between late middle Tithonian and early Berriasian in age (Armella *et al*., 2007). The Picún Leufú Formation shows an increase in dinocyst diversity when compared with the Vaca Muerta Formation. Moreover, several endemic taxa, such as *Aptea notialis*, *Diacanthum argentinum*, *Paraevansia mammillata* and *Pilosidinium cactosum*, were defined in this formation by Quattrocchio and Sarjeant (1992).

DISCUSSION

At the global scale several authors have recognized the presence of two realms (Boreal and Tethyan) during the Early Jurassic, based on different ammonite, foraminiferal, brachiopod and calcareous nannofossil assemblages (*in* Bucefallo Palliani and Riding, 1999). From a palynological point of view, many diversified Early Jurassic dinocyst assemblages have been reported from these faunal provinces, mainly from the Northern Hemisphere. Some of these citations include *Dapcodinium* from the Hettangian stage and *Liasidinium* from the late Sinemurian in southwestern Germany (*in* Zavattieri *et al*., 2008), *Luehndea*, *Mancodinium*, *Mendicodinium*, *Nannoceratopsis*, *Scrinocassis*, among others, from the Pliensbachian and Toarcian of many European localities (*in* Bucefallo Palliani and Riding, 1999), and the *Parvocysta* suite, including *Phallocysta*, throughout the late Toarcian of northern East Siberia (Riding *et al*., 1999). These authors postulated that a mutual exchange of taxa occurred between the Boreal and Tethyan realms since the Pliensbachian. These migrations were possible due to the opening of an epicontinental passageway between Greenland and Norway named Viking Corridor (Fig. 3). Even though it is true that the dinocyst assemblage from the Nestares Formation shares more components, at a genus level, with northern East Siberian than with north-western Australian (Riding and Helby, 2001) assemblages, it is quite different from both assemblages. The reason the southern Neuquén Basin (Alicurá Dam) assemblages are unlike any other late Toarcian dinocyst associations may probably be due to the paralic bay depositional setting of the Nestares Formation.

A plausible migration route of this marine biota might have been the Trans-Pacific route of Aberhan (2001) because the Hispanic Corridor mainly acted as a filter at this time; a latitudinal exchange surrounding Pangea would not be expected due to the presence of the Jurassic climatic zones proposed by Parrish (1992). Moreover, the absence of an active subduction zone immediately to the west of South America at this time would have allowed the trans-pacific interchange (Howell *et al.*, 2005) (Fig. 3).

In summary, the scarcity of dinoflagellate cysts during the Early Jurassic in the Neuquén Basin was probably related to the paleogeographic configuration of the basin. During the earlier Jurassic Pre-Cuyo Group the paleogeography showed the dominance of isolated rift depocenters (Vergani *et al.*, 1995; Howell *et al.*, 2005). This context partially remained for the lower Cuyo Group deposits. The interconnection among the different depocenters would have been scarce with the development of relatively small basins with variable salinity and low oxygenated water conditions. This environment was highly unsuitable for the proliferation of cyst-forming dinoflagellates (van de Schootbrugge *et al.*, 2005 and references therein). Thus, these ecological niches were colonized by green algae, including prasinophytes and acritarchs (Figs. 4, 5.1–14).

Since the late Toarcian, the isolated rift depocenters of earlier Jurassic times were gradually amalgamated into a single, broad basin. These paleoenvironmental conditions continued until the Early Cretaceous (Vergani *et al.*, 1995). The presence of this single basin allowed the development of relatively more diversified organic-walled marine microplankton assemblages (*i.e.*, acritarchs, prasinophytes and dinocysts) during the Middle Jurassic. The marine palynofloras were mainly dominated by acritarchs and prasinophytes during the Aalenian–early Callovian (Cuyo Group) when the marginal condition prevailed in the marine environment. The most diversified Jurassic dinocyst assem-

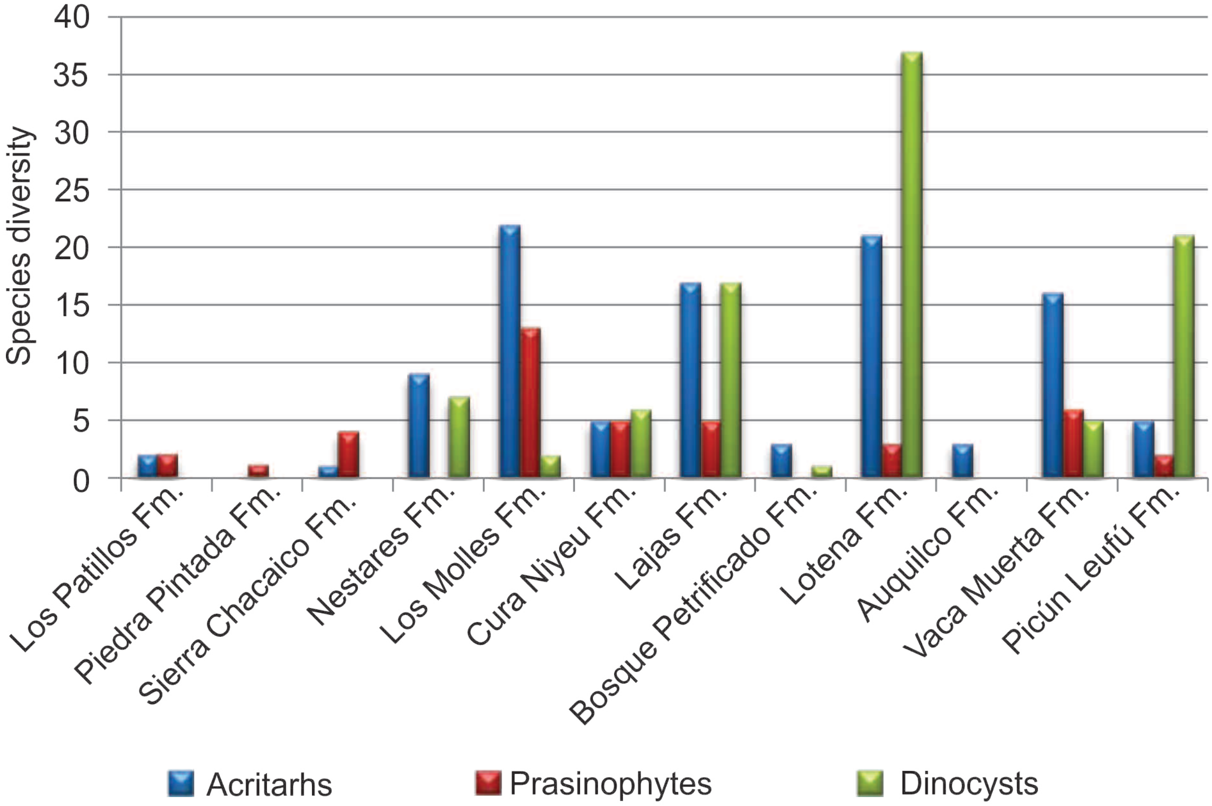


Figure 4. Histogram showing the distribution of the organic-walled marine microplankton (acritarchs, prasinophytes and dinocysts) from the units considered in this study.

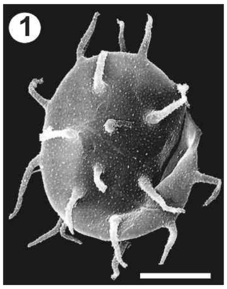
blages have been reported from the late Callovian Lotena Formation which suggests the predominance of non-restricted open marine conditions in the Neuquén Basin at that time (Figs. 4, 5.20–26, 6.1–9; Tab. 1). A similar increase in dinoflagellate cyst diversity was reported for the late Callovian sequences of Europe (Riding *et al.*, 2010). The main affinity of the Lotena dinocyst association was inferred as European, suggesting a free movement via the Hispanic seaway (Riding *et al.*, 2011) which is reinforced by the presence of some cosmopolitan forms, such as *Gonyaulacysta jurassica* (Deflandre) Norris and Sarjeant 1965 and *Scriniodinium crystallinum,* in this palynoflora (Martínez and Quattrocchio, 2004). However, the presence of *Dissiliodinium volkheimeri* Quattrocchio and Sarjeant 1992 (Fig. 5. 26) a taxon confined to the Southern Hemisphere (Riding *et al.*, 2011) is worth noting. Mantle (2009) reported its first worldwide occurrence from the northern Bonaparte Basin, Timor Sea (Australia), from the *Wanaea indotata* Interval Zone (middle Bathonian–early Callovian) through the *Voodooia tabulata* Interval Zone (late Callovian). Thus, a connection from northern Australasia to the Neuquén Basin via the Mozambique Corridor cannot be entirely ruled out.

The next widespread Paleopacific marine transgression in the Neuquén Basin consists of bituminous shales, marls and limestones of the Vaca Muerta Formation (Legarreta and Uliana, 1991, 1996). There is a decrease in dinocyst diversity and an increase in the acritarchs and prasinophyte content in the Vaca Muerta Formation compared with the Lotena Formation (Quattrocchio, 1980; Quattrocchio and Volkheimer, 1990; Quattrocchio and Sarjeant, 1992), which may be related to the anoxic to dysoxic environmental condition that prevailed during the deposition of the Vaca Muerta Formation (Figs. 4, 6.15–16.18 Tab. 1). Studies on modern dinoflagellates have shown that oxygen availability exerts a strong control on cyst germination, with anaerobic conditions completely inhibiting the excystment of most taxa (Candel *et al.*, 2013 and references therein).

It may be argued that oxygen availability is one of the most important factors in controlling the diversity and abundance of benthic biota. The relative increase in dinocyst diversity in the Picún Leufú assemblages might be correlated with a more oxygenated condition of the water column at that time, compared with the underlying formation (Figs. 4, 6.10–14.17; Tab. 1).

The distribution of the cosmopolitan and endemic taxa is influenced by the ecology of the environment (Valentine, 1973). The Picún Leufú Formation was deposited during a highstand system tract and comprises a wide range of sub-environments within the whole marginal marine system (Armella *et al.*, 2007). As mentioned by Götz *et al.* (2005) during the highstand phase, the environmental conditions stabilize and the biota becomes more diverse, therefore the main mechanism of this enrichment is speciation of endemic taxa. This context highly correlates with the presence of several endemic species recorded in the Picún Leufú strata.

Figure 5. 1–2, *Michrystridium brevispinosum*; 1, UNSP LM 1312 (from Martínez *et al.*, 2001); **2, UNSP BN 1957c** (from Olivera *et al.*, 2010); **3–4, *Michrystridium recurvatum* forma *recurvatum*; 3, UNSP LM 1312** (from Martínez *et al.*, 2001); **4, UNSP BN 1957c** (from Olivera *et al.*, 2010); **5, *Michrystridium fragile*, UNSP LM 1312; 6, *Michrystridium inconspicuum*, UNSP LM 1312; 7, *Michrystridium placophorum* UNSP LM 1312; 8, *Michrystridium echinoides* UNSP LM 1312** (5–8, from Martínez *et al.*, 2001); **9, *Baltisphaeridium* sp., UNSP LM 1312f, Efco**: R43/4; **10, *Polygonium* sp., UNSP LM 1312** (from Martínez *et al.*, 2001); **11, *Tasmanites* sp., UNSP PL 1429a; 12, *Pleurozonaria* cf. *P. picunensis*, UNSP PL 1429CAN; 13, *Cymatiosphaera* sp. 2, UNSP PL 1466a; 14, *Cymatiosphaera* cf. *C. volkheimerii*, UNSP PL 1429CAN** (11–14, from Martínez *et al.*, 2005); **15, ?Suessiaceae indet. MPLP 7235E; 16, *Parvocysta* sp. MPLP 7187A** (15–16, from Zavattieri *et al.*, 2008); **17–18, *Jansonia psilata*, UNSP LM 1312** (from Martínez *et al.*, 1999); **19, *Escharisphaeridia pocockii*, UNSP PL 1429c** (from Martínez *et al.*, 2005); **20, *Chytroeisphaeridia chytroeides*, UNSP PC 1525d, Efco**: O22/1; **21, *Wanaea acollaris*, UNSP PL 2971/2** (from Riding *et al.*, 2011); **22, *Ambonosphaera? staffinensis* UNSP PL 2970/8, EFco**: H39; **23, *Lithodinia jurassica* subsp. *reburrosa* UNSP PL 2970** (from Quattrocchio and Sarjeant, 1992); **24, *Limbodinium absidatum*, UNSP PL 2971/7** (from Riding *et al.*, 2011); **25, *Mendicodinium groenlandicum*, UNSP PL 2971/7, EFco**: E39/1; **26, *Dissiliodinium volkheimeri* UNSP PL 2970** (from Quattrocchio and Sarjeant, 1992). Scale bar= 10μm. Acronyms: UNSP (Universidad Nacional del Sur, Palinología); MPLP (Mendoza-Paleopalinoteca-Laboratorio de Palinología).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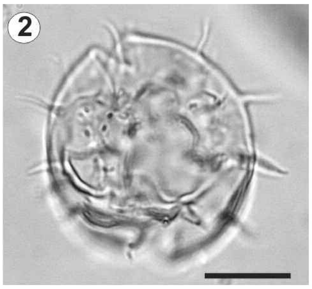
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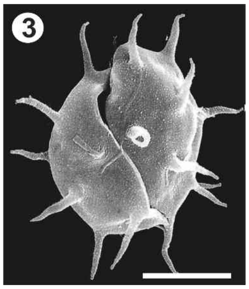
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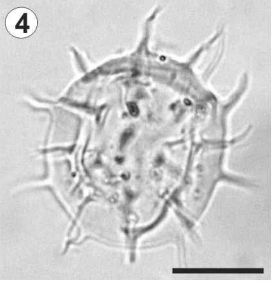
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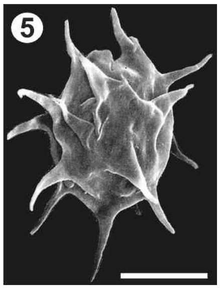
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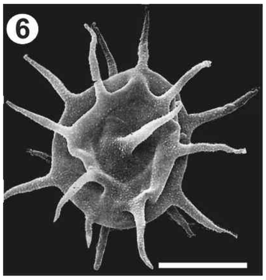
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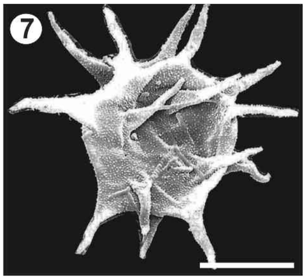
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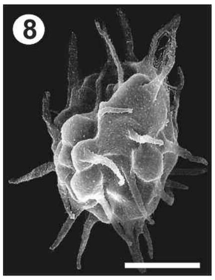
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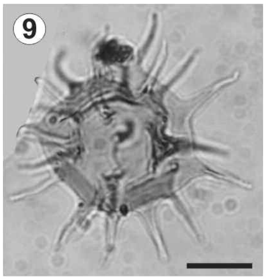
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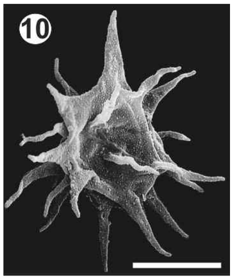
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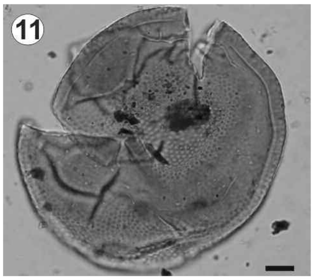
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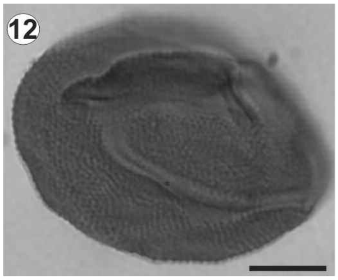
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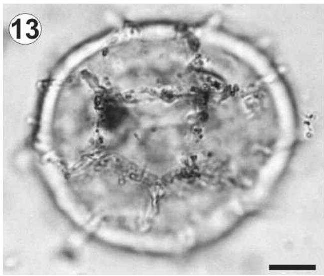
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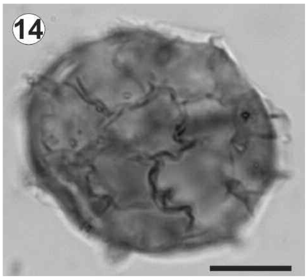
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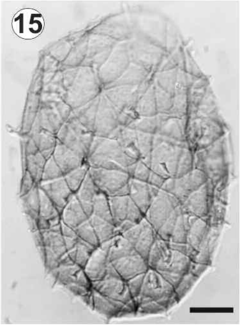
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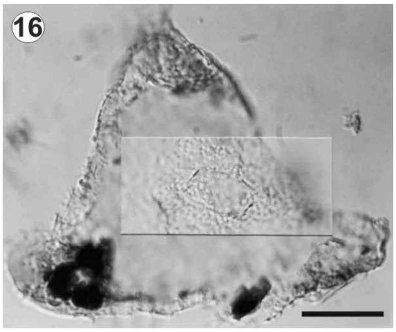
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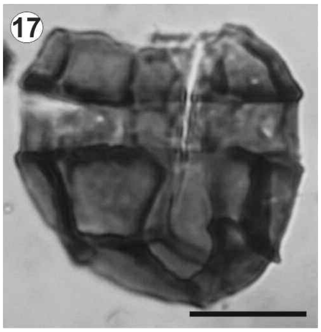
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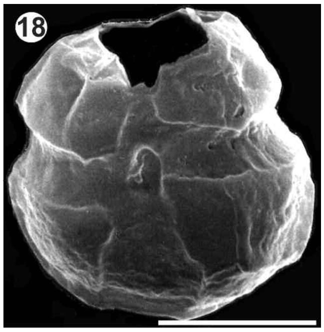
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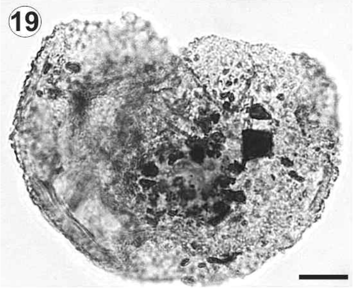
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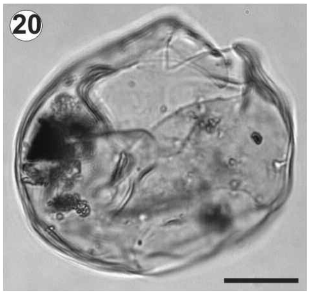
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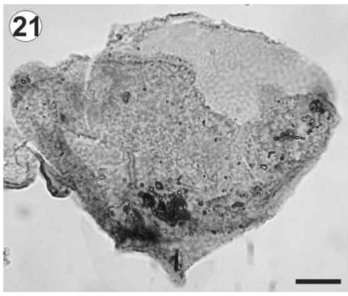
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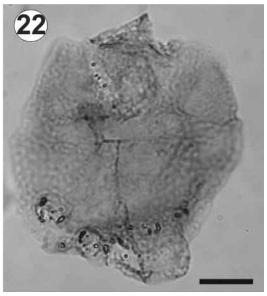
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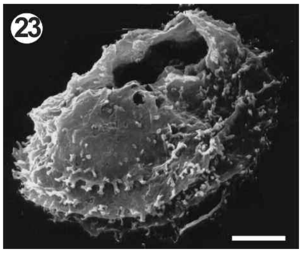
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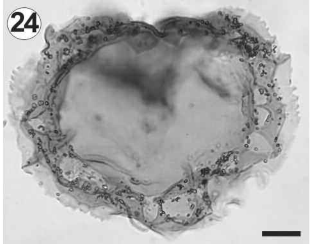
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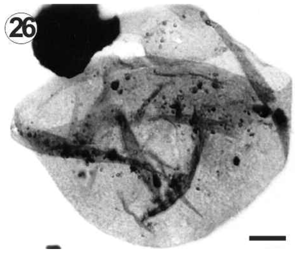
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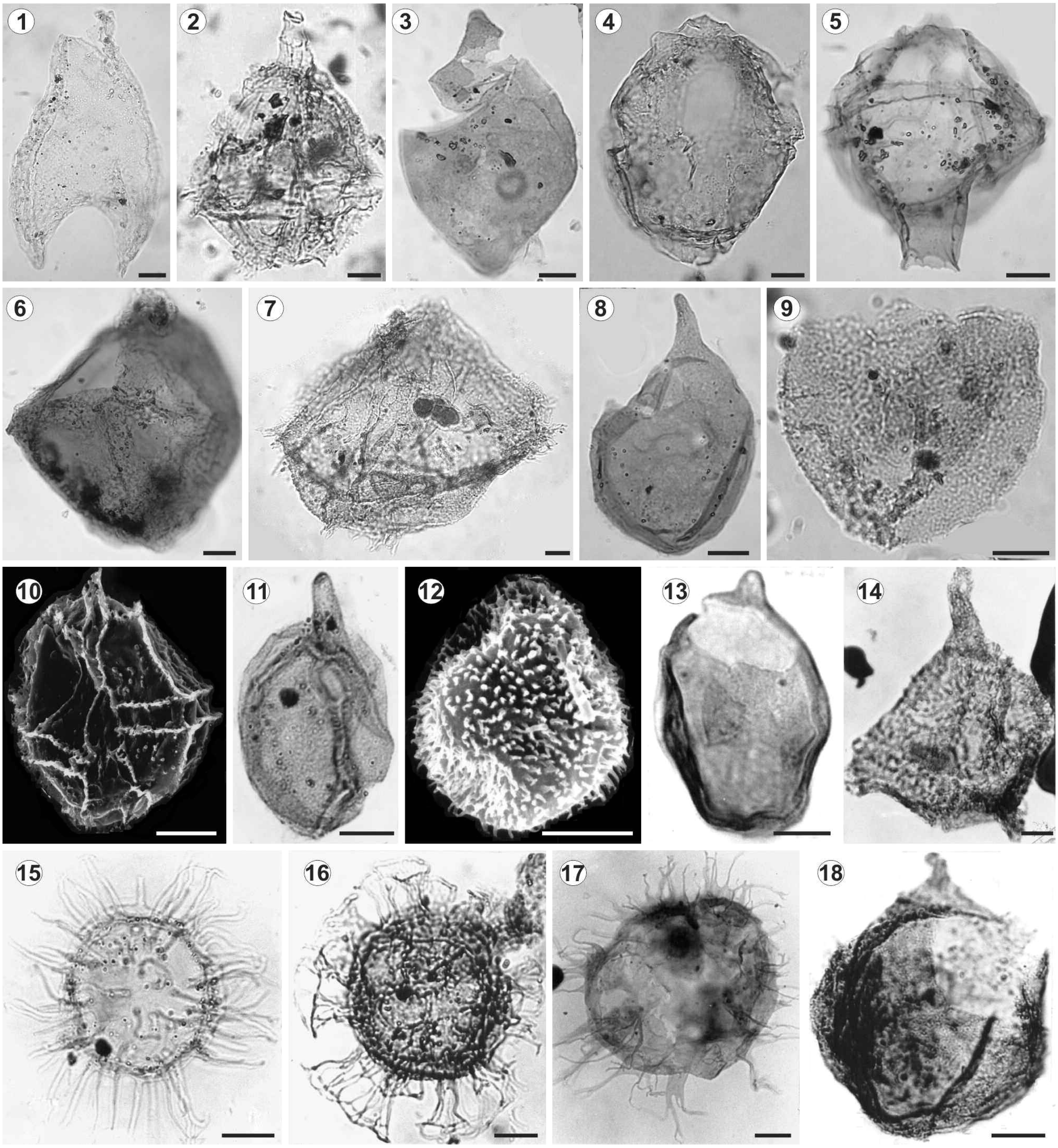

Figure 6. 1, ***Nannoceratopsis pellucida*****, UNSP PL 2971/3** (from Riding *et al*., 2011); **2,** ***Gonyaulacysta jurassica*** **subsp.** ***adecta*****, UNSP PC 1525b** (from Martínez and Quattrocchio, 2004); **3,** ***Protobatioladinium*** **cf.** ***P. lindiensis*****, UNSP PL 2971/3** (from Riding *et al*., 2011); **4,** ***Scriniodinium crystallinum*****, UNSP PC 1525c** (from Martínez and Quattrocchio, 2004); **5,** ***Tubotuberella dangeardii*****, UNSP PL 2971/7; 6,** ***Endoscrinium*** **cf.** ***E. galeritum*** **subsp.** ***reticulatum*****, UNSP PL 2971/7; 7,** ***Rynchodiniopsis cladophora*****, UNSP PC 1525d; 8,** ***Pareodinia ceratophora*****, UNSP PL 2971/4** (5–8, from Riding *et al*., 2011); **9,** ***Lithodinia deflandrei*****, UNSP BN 1959c** (from Olivera *et al*., 2010); **10,** ***Rhynchodiniopsis*** **cf.** ***setcheyensis*****, UNSP PL 2966; 11,** ***Pareodinia ceratophora*** **var.** ***pachyceras*****, UNSP PL 2965/1; 12,** ***Pilosidinium cactosum*****, UNSP PL 2966; 13,** ***Paraevansia mammillata*****, UNSP PL 2967/2; 14,** ***Aptea notialis*****, UNSP PL 2966/2; 15,** ***Cleistosphaeridium lumectum*****, UNSP PL 2970/4; 16,** ***Hystrichosphaerina neuquina*****, UNSP PL 2965/6A; 17,** ***Systematophora pinicillata*****, UNSP PL 2966/1; 18,** ***Milloudodinium nuciforme*** **UNSP PL 2969/4** (10–18, from Quattrocchio and Sarjeant, 1992). Scale bar= 10µm.

CONCLUSIONS

This paper summarizes all available marine palynological information from the Jurassic units of the Neuquén Basin and constitutes our state of the art view of this topic.

The distribution of the Jurassic organic-walled marine microplankton of the Neuquén Basin is closely related to the paleoenvironmental conditions and the configuration of the basin, as well as to the global and local ocean circulation patterns.

The Early Jurassic units are highly dominated by green algae, including prasinophytes and acritarchs, with very scarce dinoflagellate cysts. This kind of marine palynoflora could correspond to the configuration of the basin which was characterized by different depocenters with scarce interconnections. The Nestares Formation is the only exception with a relatively diversified dinocyst assemblage. A possible migration route of the cosmopolitan marine biota recovered from this unit might have been the Trans-Pacific route, due to the Hispanic Corridor which mainly acted as a filter at that time.

The diversification of the organic-walled marine microplankton recorded in Middle Jurassic units could be the result of the fusion of the Early Jurassic rift depocenters into a single late Toarcian basin, increasing the number of niches available for colonization.

During the Middle Jurassic, two main pulses of marine microplankton diversification can be recognized. In the first one (Aalenian–early Callovian), the assemblages were mainly dominated by acritarchs and prasinophytes. These palynofloras were recovered from the marginal-marine Cuyo Group deposits. The second great episode of flooding in the basin marks the beginning of the second pulse, when more open-marine conditions were established. In this context, the late Callovian Lotena assemblages exhibit the highest dinoflagellate cyst diversity of all the Jurassic units. Two possible migration routes can be recognized for the main biota interchange: the Hispanic Corridor seaway, due to the European affinity of the associations, and the Mozambique Corridor, due to the record of *Dissiliodinium volkheimeri* that was only recognized in both the Bonaparte (Australia) and Neuquén (Argentina) basins, suggesting a possible Australian connection.

The diversity of the Late Jurassic dinocyst assemblages shows a decrease in regard to the older Lotena assemblages. The anoxic to dysoxic environmental conditions that prevailed during the deposition of the Vaca Muerta Formation controlled the composition of the organic-walled marine microplankton assemblages, dominated by acritarchs and prasinophytes. On the other hand, the relative increase in dinocyst diversity of the Picún Leufú assemblages could be related to well-oxygenated and well-mixed bottom waters.

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MULTI-PROXY ANALYSIS OF LATE QUATERNARY SEDIMENTS IN THE LOWER BASIN OF THE QUEQUÉN SALADO RIVER (BUENOS AIRES PROVINCE, ARGENTINA): AN UPDATE

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Abstract. Two fossil sections (Late Quaternary), and a group of modern samples analyzed through pollen and non-pollen palynomorphs, enabled the reconstruction of the palaeoclimatic and palaeoenvironmental conditions of the lower basin of the Quequén Salado River (Buenos Aires Province). The study was complemented with analysis of sedimentology, malacofauna, ostracods, diatoms, and mammal and archaeological remains. For the Late Pleistocene, the scarce presence of microfossils, associated with eolian palaeoenvironments, allowed inferring arid/extremely arid climate conditions. In the Pleistocene/Holocene boundary, evidence of a pedogenetic event suggests a brief lapse of climatic stability. Pollen indicates the development of a halophyte steppe, which remained in the area until the Middle Holocene. During the Early Holocene (8,173 cal yr B) the sedimentology, malacofauna and microfossils evidenced a sea level rise. This event ended with the establishment of a brackish lacustrine body towards the Middle Holocene. After that, a pulse characterized by high humidity levels, indicate the replacement of the halophyte steppe by a gramineous steppe. Following that pulse during the 6,799 cal yr BP 5,603 cal yr BP lapse, the microfossils showed considerable variability, thus reflecting an alternation between relatively more humid and dry pulses. Evidence indicates that during the Late Holocene (~ 1,000 yr BP) modern ecosystems began to settle in the lower basin of the Quequén Salado River. Two global climate changes, the Medieval Climate Optimum (823 cal yr B- 690 cal yr B) and the Little Ice Age (389 cal yr B) were inferred through pollen and faunistic remains at QS$_1$ Archaeological Site.

Key words. Palaeoenvironmental-palaeoclimatic changes. Late Quaternary. Quequén Salado River. Argentina.

Resumen. ANÁLISIS MULTI-PROXY DE SEDIMENTOS DEL CUATERNARIO TARDÍO EN LA CUENCA INFERIOR DEL RÍO QUEQUÉN SALADO (PROVINCIA DE BUENOS AIRES, ARGENTINA). UNA ACTUALIZACIÓN. El análisis de microfósiles polínicos y no polínicos de dos secciones fósiles de edad Cuaternario tardío y de un conjunto de muestras actuales, permitió evaluar las fluctuaciones paleoambientales y paleoclimáticas en la cuenca inferior del río Quequén Salado (provincia de Buenos Aires). El aporte de la sedimentología, malacofauna, ostrácodos, diatomeas, restos de mamíferos y arqueológicos, complementó el estudio efectuado. Para el Pleistoceno Tardío los escasos microfósiles hallados, asociados a paleoambientes eólicos permitieron inferir condiciones climáticas áridas/extremadamente áridas. En el límite Pleistoceno/Holoceno, evidencias pedogenéticas se asociaron a un breve episodio de estabilidad climática, el polen reflejó el desarrollo de comunidades halófitas las cuales permanecieron en el área hasta el Holoceno Medio. Durante el Holoceno Temprano (8,173 cal. años AP), el ascenso del nivel marino manifestado a través de la sedimentología, malacofauna y microfósiles, culminó con la instalación de un cuerpo lagunar salobre hacia el Holoceno Medio. Con posterioridad, un pulso más húmedo inferido a partir del reemplazo de la estepa halófita por graminosa, fue seguido de un lapso (6,799 cal. años AP–5,603 cal. años AP) con alternancia de períodos húmedos y secos evidenciados a partir de una importante variabilidad en las asociaciones polínicas, los microfósiles no polínicos (MNPs), ostrácodos y diatomeas. Para el Holoceno Tardío se habrían establecido en el área los ecosistemas actuales, registrándose, en el Sitio Arqueológico QS$_1$, dos cambios climáticos globales: Óptimo climático Medieval (823 cal. años AP–690 cal. años AP) y La Pequeña Edad de Hielo (389 cal. años AP).

Palabras clave. Cambios paleoambientales-paleoclimáticos. Cuaternario tardío. Río Quequén Salado. Argentina.

Continental deposits are usually characterized by unconformities and marked facies changes. Land-based records are significantly more useful than deep-sea records in terms of spatial detail and sensitivity. Palaeoenvironmental studies have, to some degree, been avoided on arid lands due to their sparse vegetation, poor pollen production, high rates of deposition in most continental basins, predominantly clastic sediments, and abundance of carbonate and sulphate cements (Horowitz, 1992). However, these types of lands are more sensitive than temperate or tropical ones for registering environmental changes, which enables a more accurate reconstruction of global trends (Horowitz, 1992). Thus, the southern Pampean Region of Argentina clearly exemplifies the relevance of multidisciplinary studies of arid-semiarid landscapes in reconstructing the evolution of past climates (Quattrocchio *et al*., 2008).

In this region, most of the palaeoenvironmental and palaeoclimatic reconstructions of the Late Quaternary were based on the study of sections exposed along river valleys and loess sequences. Through pollen analysis Borromei (1995, 1998) studied the climatic and environmental fluctuations since the Late Pleistocene–Holocene in the Sauce Grande Valley. Grill (1995, 1997) conducted similar studies in the Napostá Grande stream basin, and Quattrocchio *et al*. (1988, 1998, 2008) carried out multi-proxy studies (sedimentology, palaeontology and micropalaeontology) in the main superficial fluvial systems southwest of Buenos Aires Province. Stutz *et al*. (1999) showed the evolution of the vegetation during the Holocene, affected by eustatic fluctuations at La Ballenera Creek.

A few studies focus on lacustrine records, among which Vilanova *et al*. (2006) stands out as it presents similar studies to those previously mentioned for the Villa Gesell headland. Fontana (2005) reconstructed the palaeoenvironments and vegetation of the Holocene in the locality of Monte Hermoso (La Olla 1 and Sauce Grande Lagoon Sites), based on pollen content, calcareous microfossils (ostracods and foraminifers) and plant microfossil remains in the sediments.

In addition, several palaeoenvironmental and palaeoclimatic reconstructions associated with archaeological sites have been carried out in rivers, streams and lacustrine bodies of south-western Buenos Aires Province (Zavala *et al*., 1992; Madrid *et al*., 2002; March *et al.,* 2003; Bayón *et al*., 2004; Grill *et al*., 2007, 2010; Gutiérrez and Martínez, 2008; Martínez *et al*., 2009a–c; among others).

Regarding the river valleys of the southern Pampean Region, they have sporadically functioned as zones of sediment transport from the ranges (Sierras Australes) to the continental shelf (Zavala and Quattrocchio, 2001, p. 32). Field evidence shows that these valleys, carved sometime in the Pleistocene, have acted for a long time as dried depressed areas, subject to no deposition or to aeolian deposition, or have been drained by local, ephemeral streams (Zavala and Quattrocchio, 2001). It is estimated that the age of the valley filling, associated with stages 2, 3 and 4 (Zavala and Quattrocchio, 2001, p. 35–36), is Early to Middle Pleistocene, coinciding with an interglacial period, extending until the Late Holocene, when the final incision of the streams occurred. A good example is the Quequén Salado River, one of the most important fluvial systems in south-western Buenos Aires (SE of Pampean Region).

Conversely, sequence stratigraphy models that attempt to relate the incision of valleys with relative sea-level falls might not be applied to the fluvial systems of the southern Pampean Region. For the LGM (Late Glacial Maximum), when the sea level was 120 m lower than today (Alley, 1990), there is no evidence of incision in the region (there is evidence of ephemeral deposits and palaeosoils), and it was probably the climate that played a major role in shaping the landscapes (Zavala and Quattrocchio, 2001). Hence the importance of reconstructing palaeoclimates through different “proxy data”.

The main aim of this contribution is to provide a palaeoenvironmental and palaeoclimate reconstruction of the lower basin of the Quequén Salado River (Pampean Region) from the Late Pleistocene to the present. The studies performed include multiproxy analyses: sporomorphs (spores and pollen grains), organic-walled marine microplankton, NPMs (non-pollen microfossils), sedimentological, palaeontological (malacofauna, ostracods and diatoms) and archaeological studies. Among previous geological and palaeontological research conducted in the study area, Frenguelli (1928); Farinati and Zavala (1995); Martínez and Gutiérrez Tellez (1998) and Alberdi *et al*. (1995) stand out. The only palynological studies conducted in this basin correspond to one of the authors of the present work (Grill, 2003; Grill and Lamberto, 2006 and Grill *et al*., 2010).

Grill (2003) analyzed the changes in vegetation and eustatic fluctuations from the Late Pleistocene to the present in the Estancia Thomas Profile. Grill and Lamberto (2006) studied the palynofacies in seven modern environments of the lower Quequén Salado River basin, along with the relationship between pollen and vegetation. Native and exotic elements of the existing flora were differentiated with special emphasis placed on taphonomy for the total palynological organic matter analysis. In Grill *et al*. (2010), palaeoenvironmental and palaeoclimatic fluctuations during the last 1,000 yr BP were analyzed in a stratigraphic sequence associated with a human settlement (QS_1 Archaeological Site).

In the present contribution, the previously mentioned results (fossil: Estancia Thomas Profile and QS_1 Archaeological Site, and modern samples) will be integrated, updated and reinterpreted for the first time. In addition, it is worth mentioning that new radiometric dating is provided for the most complete fossil sequence studied in this work (Estancia Thomas Profile). In turn, the global climate fluctuations inferred for the last 1,000 yr BP in QS_1 Archaeological Site are compared with data from recently studied archaeological sites in the lower basin of the Colorado River (300 km south of the Quequén Salado River) (Fernández, 2012).

Finally, it is important to highlight the relevance of the use of "modern analogues" from the vicinity of the studied fossil sequences, in the reconstruction of the evolution of past environments and climates. In this sense, modern samples from the Bahía Blanca Estuary, approximately 200 km south of the studied area (Grill and Guerstein, 1995) were used in addition to the modern samples from the lower basin of the Quequén Salado River. The data obtained from this group of samples were extremely relevant for the environmental reconstruction of the area, as they were obtained at a modern estuarine environment, which is relatively close to the fossil sequence affected by estuarine fluctuations during the Holocene.

REGIONAL SETTING

Geomorphology

The Quequén Salado River originates between two structural heights comprising the "Positivo Bonaerense" (Tandilia to the north and Ventania to the south). Its drainage area corresponds to the Pampa Interserrana (Frengüelli, 1950), which presents, just like the rest of the Pampean Region, a scarcely elevated landscape, typically flat, with no significant variations in height. It runs for 162 km and flows into the Atlantic Ocean as an estuary (Marini, 2002). It can be compared with integrated drainage networks (González Uriarte, 1984) or with R1 (main drainage networks), currently active networks flowing from the Serrano or Interserrano System to the Atlantic Ocean (Zavala *et al*., 2005). It is divided into four basins: High Basin, Sierras de Pillahuincó Basin, Middle Basin and Lower Basin (Marini, 2002) (Fig. 1.1). The Lower Basin, concerning the present work (Fig. 1.2), can be associated with Zone 2 (Schumm, 1977), where the system acts as a sort of sediment "by pass". The Quequén Salado River has permanent flow, with autochthony in the high and middle basins, and allochthony in the lower basin. Further geomorphologic features of the area include three dune belts (mobile, semi-fixed and fixed, associated with interdune depressions) and small lacustrine bodies.

Climate and Vegetation

Buenos Aires Province occupies the central-eastern portion of Argentina, between 33° and 41° south latitude. Consequently, it lies within the belt of temperate climate (Burgos, 1968). Because of its position in Argentina and South America, the oceanity factor is significant (Burgos, 1968), moderating the climate, especially near the coast. Continentality features intensify away from the coast (Verettoni and Aramayo, 1976).

As regards the pattern of winds, both in warm and cold months, the NE-SW trend is due to the activity of the South Atlantic and South Pacific anticyclones. Subantartic cold air masses from the SW and warm air masses from the north, caused by the occasional recession of the Pacific anticyclone (Burgos, 1968) also affect the climate of Buenos Aires Province. In the study area, the prevailing winds come from the north, followed by the NW (Marini, 2002). Winds from the east are less frequent but reach up to 133 km/h. The annual rainfall in the area of Marisol Beach (1995–1999) is 668.6 mm, and the mean annual temperature for the same period is 14.8 °C (Marini, 2002).

From a phytogeographic perspective, the study area is located in the Pampean Province (Austral Pampean District) (Cabrera, 1976). According to the census conducted by Grill and Lamberto (2006), in the lower basin of the Quequén Salado River, the pristine vegetation has been profoundly modified by crops, grazing and anthropic forests. Out of the 56 plant species counted, 37 are native and the rest are introduced.

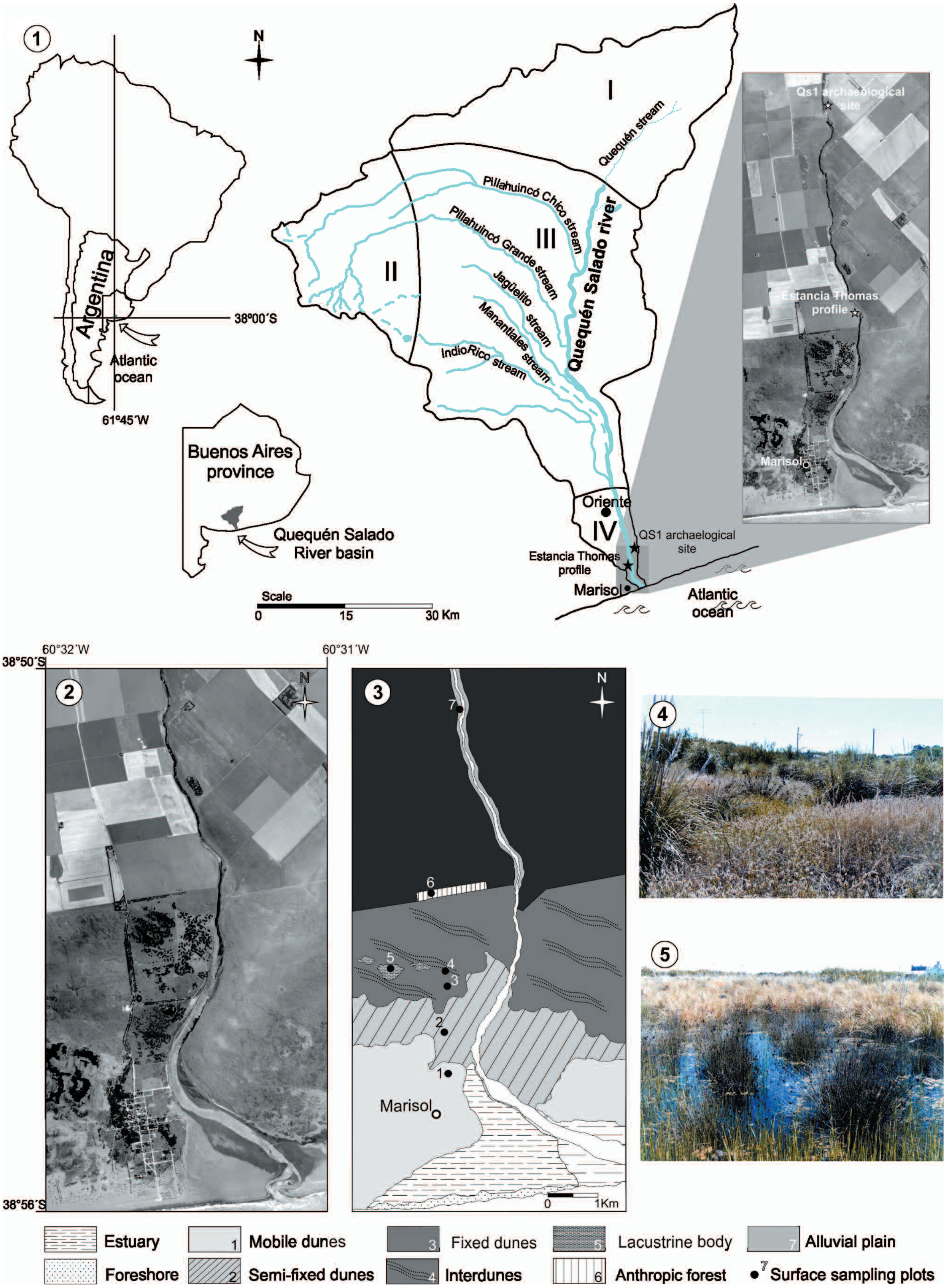

Figure 1. 1, Sectorization of the Quequén Salado River basin according to the dynamic of each area (modified from Marini, 2002): 1-High basin 2- Pillahuincó Hill 3- Middle basin and 4-Lower basin. In shaded area location of the study sites. **2,** Study area. **3,** Location map of surface sampling. **4,** Present environment of interdune pond. **5,** Present environment of lacustrine body.

TABLE 1. Vegetation and pollen spectra from surface samples of Quequén Salado river.

Sampling units	*Vegetation types*	*Pollen*
Mobile dunes	**Calycera crassifolia**, **Sporobolus rigens**, **Cortaderia selloana**	*Sterile*
Semi-fixed dunes	**Tamarix gallica**, **Sporobolus rigens**, **Cortaderia selloana**	**Tamarix gallica** *(80%)* *Poaceae (10%)*
Fixed dunes	**Hyalis argentea**, **Solidago chilensis**, **Poa lanuginosa**, **Pinus radiate***	*Poaceae (38%), Asteraceae (16%)* *Pinaceae (26,5%), Brassicaceae (4%)*
Interdunes	**Juncus acutus**, **Sporobolus rigens**,**Panicum urvilleanum**, **Lagurus ovatus**, **Hydrocotyle bonariensis**	*Asteraceae (29%), Poaceae (22%)* *Chenopodiaceae-Amaranthaceae (15,5%),* *Brassicaceae (4%)*
Lacustrine body	**Juncus acutus**, **Cotaderia selloana**, **Typha** *sp*., *Zygnemataceae,* **Scyrpus olnegi**, **Melilotus albus**	*Asteraceae (43%), Poaceae (21%) Cyperaceae, Juncaceae,* **Typha** *sp. (9%), Brassicaceae (2%)*
Anthropic forest	**Eucalyptus camaldulensis***, **E. tereticornis***, **Pinus radiata***, **P. halepensis***, **Oxalis corniculata**, **Geranium disectum**	*Myrtaceae (74%),* *Poaceae (6%), Brassicaceae (2%)*
Alluvial plain	**Lolium multiflorium**, **Festuca arundinaceae**, **Cynara carduculus***, **Cirsium vulgare***	*Presence of Asteraceae, Poaceae, Brassicaceae, Chenopodiaceae-Amaranthaceae, among others*

**introduced forest species.*

All seven environments (Fig. 1.3) characterized in this study by their plant communities and by the pollen content of their sediments are shown in Table 1. The interdune depressions and the lacustrine bodies are illustrated in Figures 1.4 and 1.5, respectively.

STRATIGRAPHY AND AGE

Reig (1957) defined the Irene Formation at the margins of the Quequén Salado River, between the localities of Irene and Oriente, which, according to Kraglievich (1960), is composed of reddish silts and clays with remains of impactites (Schultz *et al.*, 2004). Verzi *et al.* (2003, 2008) stated that the levels of this Formation that yielded remains of the Octodontidae rodent *Xenodontomys ellipticus* (Kraglievich, 1927), can be assigned to the Late Miocene.

The Estancia Thomas Profile (38° 53′ S, 60° 32′ W) represents the most complete stratigraphic column of the present study. It is located at the right margin of the river, 8 km from its mouth (Fig. 2.1). It is 4.50 m thick and is represented by four units, separated by unconformities (Farinati and Zavala, 1995). Three of them have a continental origin: Middle and Upper Sections of the Agua Blanca Sequence (Zavala and Quattrocchio, 2001), and Chacra La Blanqueada Formation (Rabassa, 1989), and one has marine origin: Las Escobas Formation (Fidalgo *et. al.*, 1973).

Due to its stratigraphic position and regional correlation, the lower section of the profile has been assigned to the Late Pleistocene. Towards the top of this section a pedogenetic event is evidenced through the record of part of its "A" horizon (Farinati and Zavala, 1995). Radiocarbon dating yielded 8,195–8,396 cal. yr BP for these levels. This dating is presumed to be the minimum age due to the rejuvenation of the sediments with soil development. In consequence it was not included in the palaeoenvironmental and palaeoclimatic reconstruction of the area. The sediments belonging to the Holocene–historical times have four radiocarbon datings covering the 8,173–207 cal. yr BP lapse. The section finishes with a paleosoil, hence, the dating (207 cal. yr BP) is considered as the minimum age due to the effect caused by the pedogenetic event.

The QS_1 Archaeological Site (38° 49′ S, 60° 32′ W) is located at the left margin of the Quequén Salado River, 11 km from the Atlantic coast (Fig. 2.2). It is represented by 1.10 m of continental sediments, assignable to the Chacra La Blanqueada Formation (Rabassa, 1989; Zavala and Quattrocchio, 2001). This section has four radiocarbon datings covering the last 1,000 yr BP.

MATERIAL AND METHODS

The fossil pollen records (Estancia Thomas Profile and QS_1 Archaeological Site; Figs. 3.1 and 3.2 respectively) were interpreted based on environmental data using the modern pollen-vegetation-climate relationship as analogue. This information was taken from Grill and Lamberto, 2006; Grill and Guerstein, 1995 (Figs. 4.1 and 4.2 respectively) and Prieto, 1996. Palynological analysis, involved identifying plant communities, their fluctuations through time and their classification into pollen assemblage zones. Relative sea level changes were evaluated in Estancia Thomas Profile, taking into account the microplankton preserved in marine deposits, as well as changes of coastal vegetal communities. Non-pollen microfossils (NPMs) were used to complement the palaeoenvironmental reconstruction, especially in the case of sterile palynological samples or when the samples did not reach the minimum number of pollen grains for analysis.

The NPMs remains found in QS-2c Pollen Subzone (Estancia Thomas Profile) represent the most conspicuous forms in the profile, and they are illustrated in Figure 5. The "multi-proxy" analysis performed in the lower basin of the Quequén Salado River, with its corresponding palaeoenvironmental and palaeoclimate inferences, are illustrated in Table 4.

The radiocarbon datings presented in this work were performed at the NSF-Arizona Laboratory (Tab. 2). All the radiocarbon ages are expressed as years BP (years Before Present) and cal. years BP (calibrated years Before Present) with a precision of ± 2σ (Stuiver *et al.*, 2005) (Tab. 3), and the mean calibrated ages are used in the text.

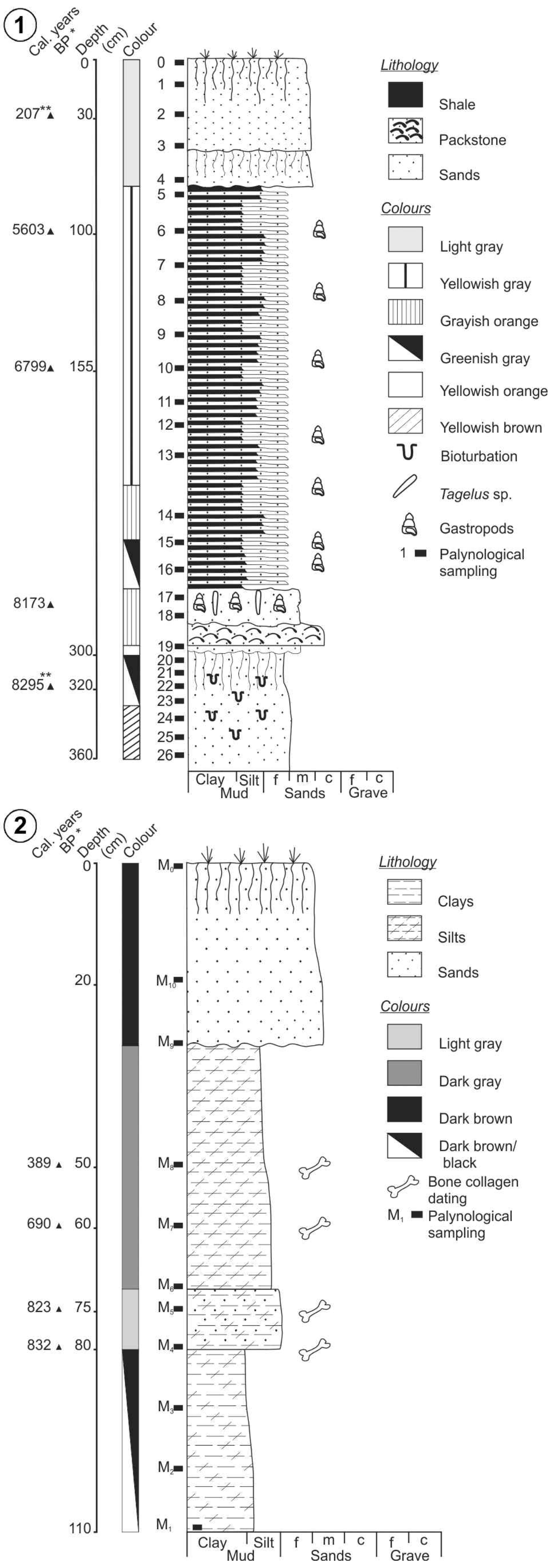

Figure 2. Stratigraphic profiles with details of the palynological sampling. **1,** Estancia Thomas Profile (modified of Farinati and Zavala, 1995) (*average age calibrated). **2, QS_1 Archaeological Site** profile (from Grill *et al.*, 2010).

TABLE 2. Radiocarbon datings presented in this work.

Depth	Laboratory Code	Sample	^{14}Cyears BP	Cal. Years BP*	δ^{13}C0/00
0.30 m (2)	AA-100392 26	sediments	182±39	131–283	-22.7
1.00 m (6)	AA-100393 21	sediments	4,905±60	5,466–5,740	-21.3
1.55 m (10)	AA-100394 17	sediments	6,004±49	6,670–6,929	-19.1
3.20 m (22)	AA-100395 5	sediments	7,542±50	8,195–8,396	-20.5

*(2) palynological samples, *Calibrated with CALIB 7.0 at 2σ (Stuiver* et al., *2005)*

TABLE 3. Radiocarbon dating used in the work.

Profile	Sample	^{14}C years BP	Cal. years B.P*	References
Estancia Thomas	Sediments	182±39	131-283	This paper
QS1 Archaeological Site	**Lama guanicoe** (Müller, 1776) (bone)	360±40	305-474	Madrid et al. (2002)
Lobería I	Mamal (bone)	440±60	320-526	Rabassa et al. (1989)
QS1 Archaeological Site	**Lama guanicoe** (bone)	790±40	642-738	Madrid et al. (2002)
QS1 Archaeological Site	**Lama guanicoe** (bone)	940±40	734-912	Madrid et al. (2002)
QS1 Archaeological Site	**Lama guanicoe** (bone)	960±40	746-919	Madrid et al. (2002)
La Toma	Vertebrate (bone)	995±65	735-960	Rabassa et al. (1989)
Estancia Thomas	Sediments	4,905±60	5,466-5,740	This paper
Sauce Grande	Sediments	5,010±120	5,465-5,949	Borromei (1992)
Estancia Thomas	Sediments	6,004±49	6,670-6,929	This paper
Sauce Chico	Sediments	6,170±170	6,638-7,417	Prieto (1989)
Estancia Thomas	**Tagelus plebeius** (shells)	7,720±100	7,975-8,371	Farinati and Zavala (1995)
Pehuen-Có	Sediments	12,000±100	13,560-14,065	Aramayo and Manera de Bianco (1996)
Pehuen-Có	Vertebrate (bone)	16,440±320	18,995-20,535	Aramayo (1997)
Castelar	Sediments	20,180±180	23,724-24,721	Grill and Morrás (2010)

**Calibrated with CALIB 7.0 at 2σ (Stuiver* et al., *2005)*

RESULTS AND DISCUSSION

Late Pleistocene

The sediments corresponding to this age, (Estancia Thomas Profile) (Agua Blanca Sequence, Middle Section) (Zavala and Quattrocchio, 2001), are composed of poorly sorted, yellowish to greyish fine sandstones (10YR6/2 to 5

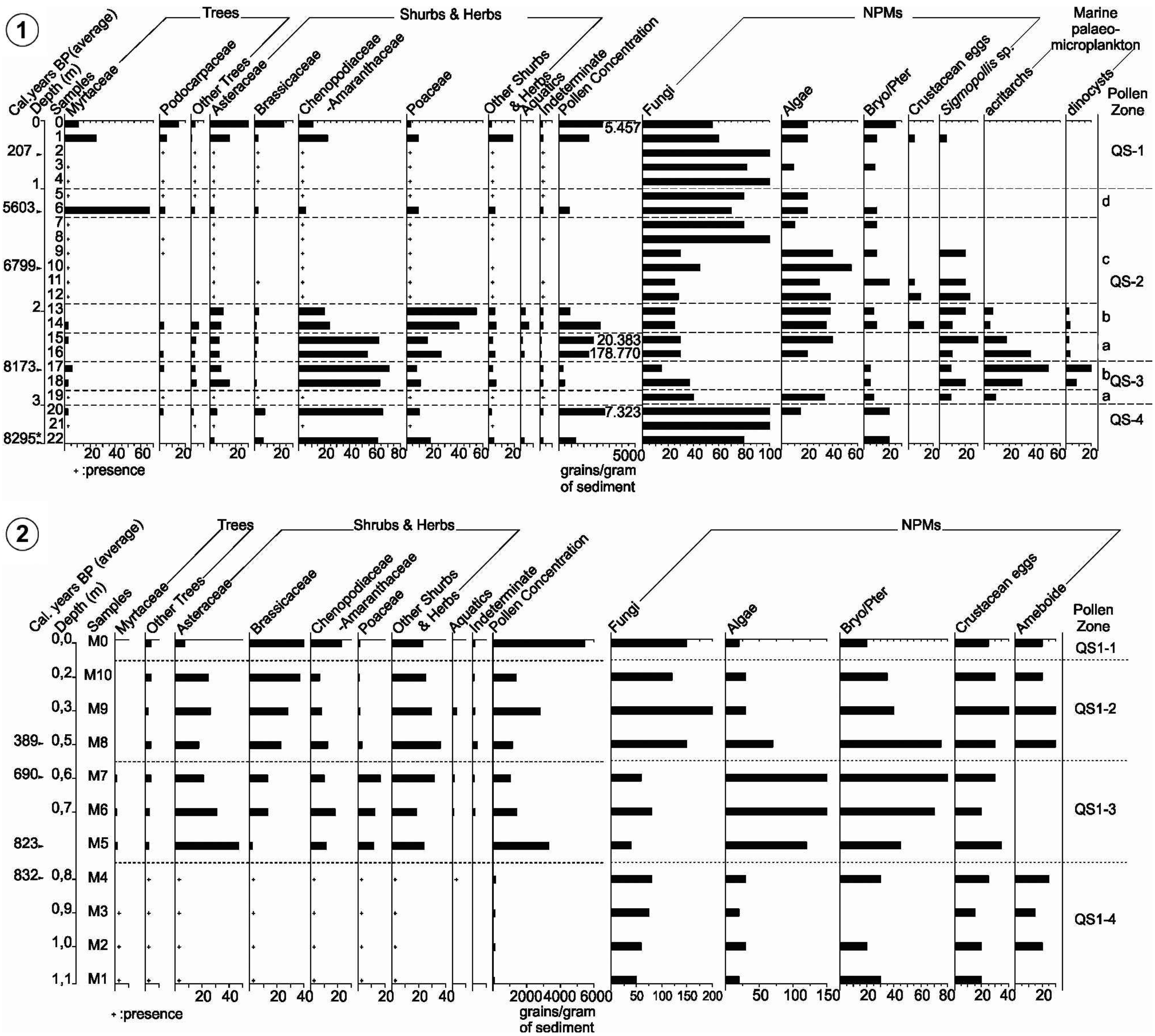

Figure 3. Non pollinic and pollinic frequency diagram of fossil samples: **1,** Estancia Thomas Profile (modified from Grill, 2003). **2, QS$_1$ Archaeological Site** profile (modified from Grill *et al*., 2010).

GY6/1), 1.30 m thick, with considerable bioturbation due to radicular activity. The upper 20 cm contain a dark green bank of sandstones (5Y2/1) with more intense bioturbation. Due to the absence of primary sedimentary structures and according to regional data, these deposits are related to aeolian dynamics (Farinati and Zavala, 1995). Afterwards, during a more stable period, there is evidence of soil development, of which only part of its "A" horizon was preserved.

At the bottom of the Agua Blanca Sequence, Middle Section, the palynological samples turned out barren (Grill, 2003). Presumably, adverse factors such as chemical oxidation under arid conditions and an alkaline environment hindered the preservation of palynomorphs (Dimbleby, 1985). Horowitz (1992) suggests that extremely arid climates prevent the development of plant cover in the resulting landscape.

Barren pollen samples have been recorded in other Late Pleistocene profiles of the south of the Pampean Region,

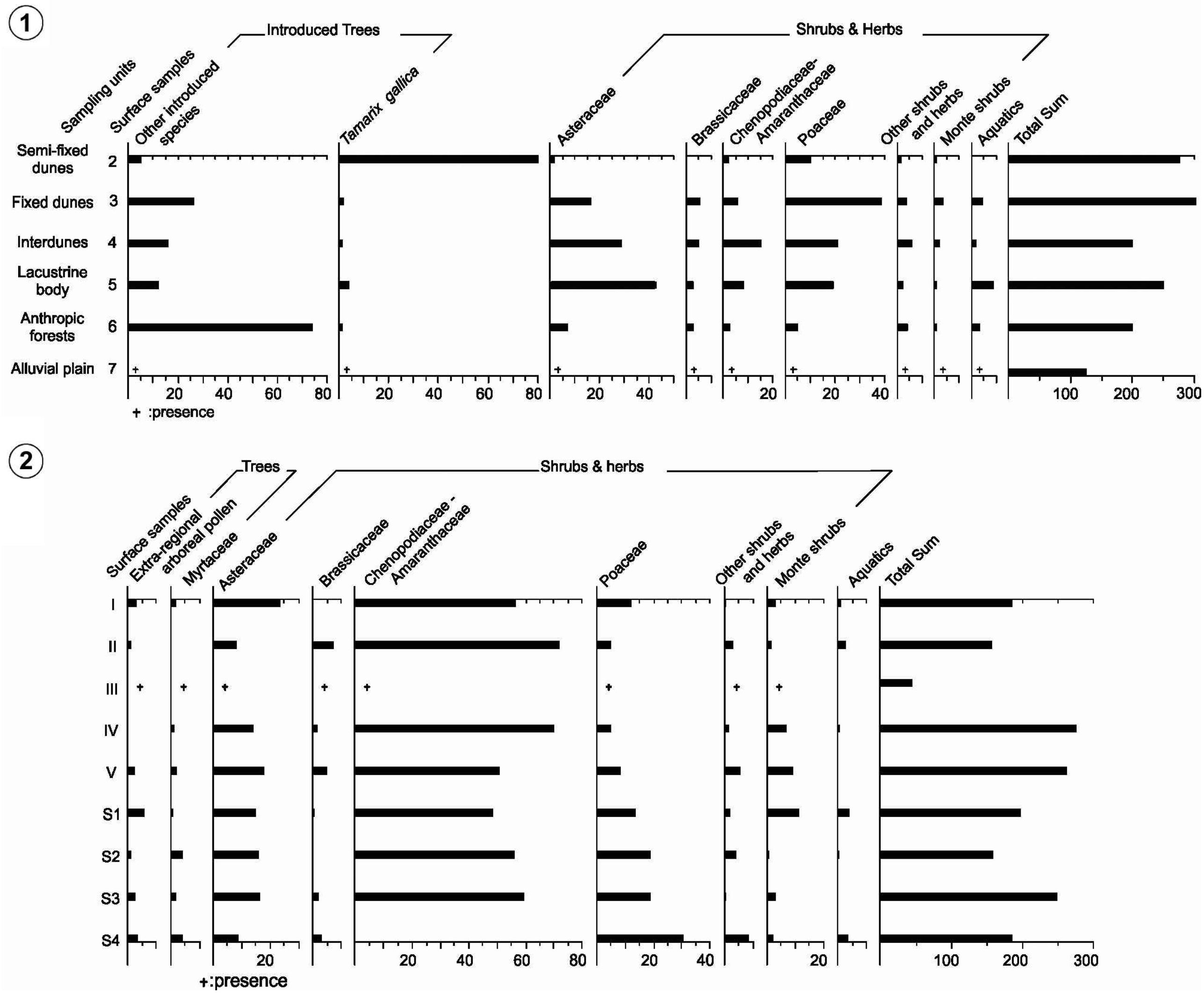

Figure 4. Pollen frequency diagram of surface samples: **1,** Quequén Salado River (modified from Grill and Lamberto, 2006). **2,** Estuary of Bahía Blanca (modified from Grill and Guerstein, 1995).

such as the Napostá Grande Stream (Grill, 1993, 1995) and the Quequén Grande River (Grill *et al.*, 2007). Commonly, the remaining pollen assemblages from this age have predominantly been associated with the Brassicaceae family. The development of these weeds may imply environmental disturbance, caused by aridity and strong eolian activity, which may have also caused the retraction of grasslands (León and Anderson, 1983).

In accordance with the sedimentology and pollen analysis, Martínez and Gutiérrez Tellez (1998) recorded scarce ostracods and diatoms at Estancia Thomas Profile for this geological moment, thus inferring severe environmental conditions.

Such climate conditions could be related to a lower sea level than the inferred for the Pehuen-Có Palaeoicnological Site, in the coast of Buenos Aires Province (100 km south of Quequén Salado), where alluvial plain sediments were dated in 13,812 cal. yr BP (Aramayo and Manera de Bianco, 1996), and a bone remain was dated in 19,765 cal. yr BP (Aramayo, 1997).

North of the Pampean Region (Undulated Pampa), studies of palynofacies associated with loess sediments suggested arid conditions for the Late Pleistocene (Grill and Morrás, 2010), although they indicate a slightly older episode (24,222 cal. yr BP) than that recorded for the Quequén Salado River. SE of Buenos Aires Province (near Mar del Plata), Zárate (1991) stated that, between LGM and 10,000 yr BP, there was an obliteration in the main valleys of the region as a consequence of aeolian activity.

Towards the top of this unit (Late Pleistocene/Holocene transition) and in connection with the recorded pedogenetic event, pollen spectrums dominated by Chenopodiaceae (64%) were found (**QS-4 Pollen Zone**) (Grill, 2003), which are analogous to those obtained by Grill and Guerstein (1995) in pollen surface samples in Bahía Blanca Estuary. These spectrums evidence areas colonized by halophytic steppes (Verettoni, 1961). These types of plant communities are typical of coastal marine and continental environments with highly saline levels.

Considering the low pollen concentration, the scarce diversity of pollen and the exiguous palaeosoil associated, this part of the sequence can be interpreted as a brief episode of climatic stability indicating relative climate improvement.

The pedogenetic event recorded at the Estancia Thomas Profile might be correlated with the Puesto Callejón Viejo palaeosoil (Fidalgo *et al.*, 1973), which covers a wide extension of the Pampean Region and appears frequently decapitated or is scarcely developed (Borromei, 1995, 1998; Grill, 1995, 1997; Quattrocchio *et al.*, 2008, among others).

Early Holocene

During the Early Holocene, after an erosive unconformity, a rise in the sea level was evidenced in the area through the sedimentology and the content of gastropods and palynomorphs.

This part of the sequence is assigned to the Las Escobas Formation (Fidalgo *et al.* 1973). It is composed of 0.35 m of thick and thin bioclastic deposits, finning and thinning upwards, in which three marine sedimentary facies were recognized, "A", "B" and "C" (Farinati and Zavala 1995).

Facies type "A" is a massive tabular body (2–4 cm thick) of well-sorted, yellowish orange middle-sized sandstones. It is interpreted as a transgressive residual deposit (Swift, 1968; Posamentier and Allen, 1993). Such deposit is associated with a progression of the coastline into the continent (Farinati and Zavala, 1995). In this facies, **QS-3a Pollen Subzone** (Grill, 2003) is characterized by scarce pollen grains and evidences the destruction of littoral communities following a transgressive event, which is further evidenced by the presence of *Micrhystridium* sp. and *Cymatiosphaera* sp. acritarchs.

Facies type "B" is characterized by an irregular tabular body (10–20 cm thick), comprised of skeletal accumulations of mollusc shells *Ostrea spreta* (d´Orbigny, 1846), *Brachidontes rodriguezi* (d´Orbigny, 1846) and *Tagelus plebeius* (Lightfoot, 1786) with diffuse horizontal lamination and a matrix of medium-sized/very thick sand. This facies is interpreted as evidencing an accretion process in a foreshore environment (Heward, 1981; Farinati and Zavala, 1995).

Facies type "C" consists of poorly selected fine/medium-sized sandstones comprising a 20 cm thick tabular body. It has dispersed gastropods and *Tagelus plebeius* valves in living position (Farinati and Zavala, 1995). Radiocarbon dating on the *Tagelus plebeius* valves yielded (8,173 cal. yr BP). This facies is interpreted as the consequence of an accretion event in a mixed flat plain environment (Erikson *et al.*, 1981; Farinati and Zavala, 1995).

The pollen spectrum of Facies "B" and "C" is mainly characterized by Chenopodiaceae (67.5%) (**QS-3b Pollen Zone**) (Grill, 2003), while the marine palaeomicroplankton is characterized by the acritarchs *Micrhystridium* sp. (Deflandre, 1937), *Cymatiosphaera polonica* (Górka, 1974) and *Cymatiosphaera* sp. (Wetzel, 1933) and, to a lower extent, by *Spiniferites* (Mantel, 1985) dinoflagellate cysts.

All the recorded palynomorphs (pollen and marine palaeomicroplankton) are similar to those documented in the modern samples of Bahía Blanca Estuary (Grill and Guerstein, 1995). The genus *Spiniferites* has also been identified in modern neritic environments (Wall *et al.*, 1977). In fossil samples, both the acritarchs and the dinoflagellate cysts suggest estuarine and neritic environments (Staplin *et al.*, 1965; Sarjeant *et al.*, 1987; among others).

The low diversity and proportion of marine microplankton, as compared to the total amount of palynomorphs, suggest unsuitable environments for the preservation of the specimens, considering the thick granulometry of the sediments, the moderate-high energy of the tidal action (Facies "B") and the occasional storms (Facies "C") (Farinati and

Zavala, 1995). At the same time, the low diversity and proportion of cysts over the number of acritarchs illustrates restricted marine environments (Gibson *et al.*, 1980).

The NPMs, *Glomus* sp. and *Botryococcus* sp., indicate relatively arid pulses. *Glomus* sp. is particularly indicative of erosive processes which are active in neighbouring areas (Medeanic *et al.*, 2008), and *Botryococcus* sp. is typically associated with brackish-water oligotrophic environments, typical of littoral areas such as lagoons and intertidal marshes (Guy-Ohlson, 1992; van Gell and Aptroot, 2006; Medeanic *et al.*, 2008). Pteridophyte spores indicate locally humid strata.

In the same profile at Estancia Thomas, Martínez and Gutiérrez Tellez (1998) recorded populations of ostracods and diatoms in which littoral marine species are dominant (the ostracods *Cytherura dimorphica* Bertels and Martínez, 1997, *Leptocythere* sp., *Perissocytheridea* sp. and *Semixestoleberis debueni* Hartmann, 1962, and the diatoms *Actinoptychus splendens* Shadbolt, 1854, *Actinoptychus senarius* Ehrenberg, 1843 and *Triceratium* sp. Ehrenberg, 1839). From Facies “A” to “C”, the relative frequencies and the diversity of marine species decrease, while limnic species increase.

The palynomorphs identified in Facies “A”, “B” and “C” evidence the permanence of subhumid-dry conditions, developing in the area since the Pleistocene/Holocene transition. Some of the NPMs indicate brief arid pulses.

The transgressive event described herein ends at the Estancia Thomas area, with the settlement of a brackish lacustrine body. Since the transgression flooded the Pleistocene valley, the decreasing energy and the final restriction would respond to the evolution of a littoral barrier at the limits of the palaeovalley, thus interrupting the connection between the marine deposits and those recorded later (Farinati and Zavala, 1995).

Middle Holocene

The foresaid lacustrine sediments from the Upper Section of the Agua Blanca Sequence (Zavala and Quattrocchio, 2001) were deposited on top of an erosive unconformity. They are 2.20 m thick and comprise decreasing layers of sand and pelites, with Characeae oogonia and a large amount of shells of *Heleobia australis* (d’Orbigny, 1835), among others (Farinati and Zavala, 1995). The presence of this last estuarine species, with high phenotypic plasticity and an optimal habitat for mesohaline gradient (8–18‰), suggests a significant level of salinity, though insufficient to reach typical marine levels (Aguirre and Fucks, 2004).

In this part of the stratigraphic sequence, the palynomorphs and NPMs are considerably variable in diversity and concentration of the different taxa. As a consequence, **QS-2 Pollen Zone** has been subdivided into 4 Pollen Subzones (QS-2a, b, c, and d) (Grill, 2003).

The lower part (**QS-2a and b Pollen Subzones**) evidences a continuity of the halophyte communities developing in the area since the Pleistocene/Holocene transition (**QS-2a Pollen Subzone**), replaced later by grass communities (Poaceae 48%) (**QS-2b Pollen Subzone**), thus indicating relatively more humid conditions, similar to those currently characterizing the plains and wetlands at the eastern and southeastern Pampean Region (Prieto, 1996). The presence of scarce marine microplankton (*Micrhystridium* sp., *Micrhystridium balmei* Sarjeant, 1973 and *Spiniferites* sp.) indicates that, in its dropping to the current position, the sea invaded occasionally some areas of the basin.

Inland, in other fluvial systems close to the Quequén Salado, relatively more humid conditions were recorded. These were associated with hydrophytic communities related to lacustrine bodies (Sauce Chico stream) (7,027 cal. yr BP) (Prieto, 1989) and, in somewhat younger sediments, to the grass steppe (Sauce Grande River) (5,707 cal. yr BP) (Borromei, 1992).

The top of the sequence (1.60 m thick) shows a significant change in microfossil content. At **QS-2c Pollen Subzone** (6,799 cal. yr BP) only a few pollen taxa were recorded, indicating shallow brackish flooding surfaces. Among them, Corticiaceae, *Glomus* sp., *Botryococcus* sp., *Spirogira* sp. and *Sigmopollis* sp., 28 types of spores (van Geel *et al.*, 1982/1983) and crustacean eggs (Fig. 5) stand out. *Glomus* sp. is a common microfossil identified among the NPMs of the southern Brazilian coast during arid periods of the Holocene regressive stages (Medeanic *et al.*, 2008). *Spirogira* sp., *Sigmopollis* sp. and completely oxidized tracheid remains evidence fluctuations in the water level. The environmental characteristics presumably unfavoured the preservation of the pollen grains in this part of the sequence.

The predominance of *Lymnocythere* sp. (94%) and the presence of the *Surirella striatula* (Turpin, 1828) and *Campylodiscus clypeus* (Ehrenberg ex. Kützing, 1844) (**QS-2b Pollen Subzone** and part of **QS-2c Pollen Subzone**) suggest the development of an oligo-mesohaline brackish littoral lagoon (Martínez and Gutiérrez Tellez, 1998). For the rest of **QS-2c Pollen Subzone**, the alternance of planktonic diatoms (*Hyalodiscus laevis* Ehrenberg, 1845*)* and benthic diatoms (*Surirella striatula*) evidences variable precipitations and ongoing water level fluctuations in the developing water bodies.

This Pollen Zone ends with **QS-2d Pollen Subzone** (5,603 cal. yr BP), dominated by Myrtaceae (50%). The dominance of this taxon over the typical herbaceous-shrubby components of the steppe and the low pollen concentrations suggest an increase in the sedimentation rates due to intense erosive processes (**QS-2c Pollen Subzone**), which apparently intensified during this stage. The Myrtaceae family, with characteristics extra-regional for the Pampean Region, indicates the persistence of considerably intense air masses, probably from the woodlands of southern Brazil and northern Argentina.

Pollen spectrums with high proportions of Myrtaceae belonging to the Middle/Late Holocene have been recorded in other alluvial basins of southern Buenos Aires (Grill, 1993; Fernández, 2012).

As regards eustatic fluctuations during the Early/Middle Holocene, plentiful evidence suggests that this event spread throughout the Atlantic coast, affecting not only the Buenos Aires littoral area (Grill and Quattrocchio, 1996; Fontana, 2005; Olivera *et al*., 2006; Vilanova *et al*., 2006, among others) but also southern Brazil (Grill and Medeanic, 2004; Medeanic and Correa, 2007, among others).

Late Holocene–historical times

The last 1,000 yr BP, very well represented in the QS_1 Archaeological Site, are comprised by alluvial sediments from the Quequén Salado flood plain (Farinati and Zavala, 1995). These sediments are assigned to the Chacra La Blanqueada Formation (Rabassa, 1989; Zavala and Quattrocchio, 2001).

The 1.10 m thick sequence starts with 30 cm of dark-brown clayey silt which yielded 832 cal. yr BP towards the top. In **QS_1-4 Pollen Zone**, only the presence of pollen grains, abundant fungal spores (Corticiaceae Microthyriaceae, *Monosporites* sp., *Dicellaesporites* sp., *Pluricellaesporites* sp., *Dictyosporites* sp., and *Glomus* sp.) among others, and, to a lower extent, algae spores (type 181 and 128 A/B) (van Geel *et al*., 1982/1983) and Bryophyte (*Anthoceros* sp., *Phaeoceros* sp., *Riccia* sp.) were recorded (Grill *et al*., 2010).

In the palynofacies study of modern sediments from the Quequén Salado flood plain (sample 7), palynomorphs were characterized by a scarce proportion of pollen grains, similarly to QS_1-4 Pollen Zone, evidencing a considerable damage due to mechanical influence, and chemical and biological oxidation (Grill and Lamberto, 2006).

Pollen assemblages from archaeological sites which are seasonally flooded become more easily altered or barren than those belonging to constantly dry or humid sites (Bryant and Holloway, 1983). This condition is related to the mechanical damage undergone by pollen grains as a consequence of the alternating humidity and drought periods, which, in turn, enables biological activity (by bacteria and fungus) and, in time, leads to pollen destruction.

Regarding the NPMs recorded in this Pollen Zone, the higher proportion and diversity of fungal spores in relation to algae spores indicates that the exposure periods were longer than the flooding periods, the first being more resistant to droughts than the latter (Medeanic and Silva, 2010). In addition, Bryophyte *Riccia* sp, *Phaeoceros* sp and *Anthoceros* sp. spores ratify the locally humid environments in the proximities to the runoff, and the last two have also been currently related to cultivated fields (Hässel de Menéndez, 1962, 1979). For the moment, this hypothesis is disregarded for the analysis, as there is no concrete evidence of agricultural development in the region (Grill *et al*., 2010).

In relation to the conditions of periodic humidity, these are assumed to have influenced the criteria for human settlement at the river neighbouring area. There is evidence to posit that, in dry periods, flooding plains were the environment preferred for human settlement. Due to the proximity to the river and considering the regional arid conditions, this choice was favourable during large-mammals hunting seasons, which is corroborated at QS_1 Site by the significant proportion of archaeological remains found in the sediments (Grill *et al*., 2010).

In concordance with the results obtained for the Quequén Salado lower basin, periods with important aeolian activity were recorded NE and S of the Pampean grasslands. These were associated with numerous short, dry episodes during the Late Holocene (Zárate *et al.*, 2000; Muhs and Zárate, 2001).

QS_1-3 Pollen Zone (823-690 cal. yr BP) (Grill *et al.*, 2010), involving 10 cm of sandy siltstone, presents a pollen assemblage similar to the surface pollen samples from the current fixed dunes and interdunes at the Quequén Salado lower basin (Grill and Lamberto, 2006) (samples 3 and 4, Fig. 4). However, it has a higher proportion of Brassiaceae. These communities reflect the development of a psammophyte herbaceous steppe (Verettoni, 1965; Verettoni and Aramayo, 1976). In this Pollen Zone, the highest proportion of Poaceae in the profile was recorded, along with the broadest diversity of pollen from the "shrubby forest". Accordingly, a high proportion of NPMs was found, with algae spores (*Zygnema* sp., and others) and Bryophyte (*Phaceros* sp., *Anthoceros* sp.) outnumbering fungal spores.

This Pollen Zone is also characterized by having the highest number of vertebrate remains, mainly mammals, in the sequence (*e.g.* even-toed ungulates, mostly *Lama guanicoe* Müller, 1776), with sediments marked by a strong anthropic activity (Grill *et al.*, 2010). Among the vertebrates were Brazilian elements like the rodent *Cavia aperea* (Erxleben, 1777).

A relative improvement in the climatic conditions is inferred for this geological moment on the basis of the pollen assemblage, the NPMs (the higher proportion of algae spores over fungal spores) and the fossil vertebrates.

At La Toma Archaeological Site (about 180 km from the study area), the vertebrates (847 cal. yr BP) were also of Brazilian lineage indicating warmer climate (*Dasypus* Linneo, 1758 and *Cavia aperea*) (Rabassa *et al.*, 1989).

Accordingly, in sediments dated in 1,000–500 yr BP at El Tigre Archaeological Site (approximately 300 km south QS_1), the NPMs also record a significant proportion of zygnematales (*Spirogira* sp. and *Mougeotia* sp.) (Fernández, 2012), along with the presence of the sigmodontine rodent *Holochilus brasiliensis* (Desmarest, 1819) (Stoessel *et al.*, 2008).

These data from the QS_1, La Toma and El Tigre sites suggest an improvement of the regional climate, coetaneous to the global Medieval Climatic Optimum (Rabassa *et al.*, 1989).

From 389 cal. yr BP to present time, the last 70 cm of the QS_1 Site profile involve the presence of dense and compact siltstone ending in the modern soil. The pollen spectrums (**QS_1-2 and QS_1-1 Pollen Zones**) (Grill *et al.*, 2010) are dominated by the family Brassicaceae (average of 43%), with an abrupt decrease of the family Poaceae (<2%) and aquatic plants (<1%).

In the pollen spectrums of modern samples from the Quequén Salado River, the family Brassicaceae reaches a maximum representation of 4% (Grill and Lamberto, 2006), as in other superficial samples from the Pampean Region (wet and dry Pampa), where the values oscillate between 6 and 9%, respectively (Prieto, 2000). However, it reaches 26% at the xerophitic woodland-grassland ecotone, thus suggesting that semi-arid climates are necessary for the development of these weeds (Prieto, 2000). In the same way, in disturbed environments or in dunes dominated by *Cakile maritima* (Scopoli, 1772), the values oscillate between 59% and 45% (Stutz, 1996; Fernández, 2012).

Approximately 300 km south of QS_1 Site, at the Loma Ruiz archaeological Site, pollen spectrums (last 2,000 yr BP) showed resemblance to those from QS_1, although Loma Ruiz presented higher proportions of Brassicaceae (70% on average). In these environments, associated with dunes and herbaceous psammophytic grassland, the predominance of Brassicaceae was interpreted as evidence of the environmental disturbance of the site caused by the repeated departures of the inhabitants (Fernández, 2012).

At the Lobería I Archaeological Site, approximately 170 km from the study area, the mammal fauna (dated in 423 cal. yr BP) indicated a climatic deterioration correlatable to the Little Ice Age (Rabassa *et al.*, 1989).

Further evidence of the Little Ice Age in the Pampean Region, obtained through the study of mammals, suggests dry and arid conditions around 449 years BP (Tonni *et al.*, 1999), with a more benign pulse around 300 years BP (Pardiñas and Tonni, 2000), which indicates that there were climatic variations on the secular scale in this region. Based on historical data, Moncaut (2001) analysed floodings and droughts during the 1,576–2,001 lapse, stating that the droughts were particularly strong during the Little Ice Age. Laprida and Valero Garcés (2009) identified a marked salini-

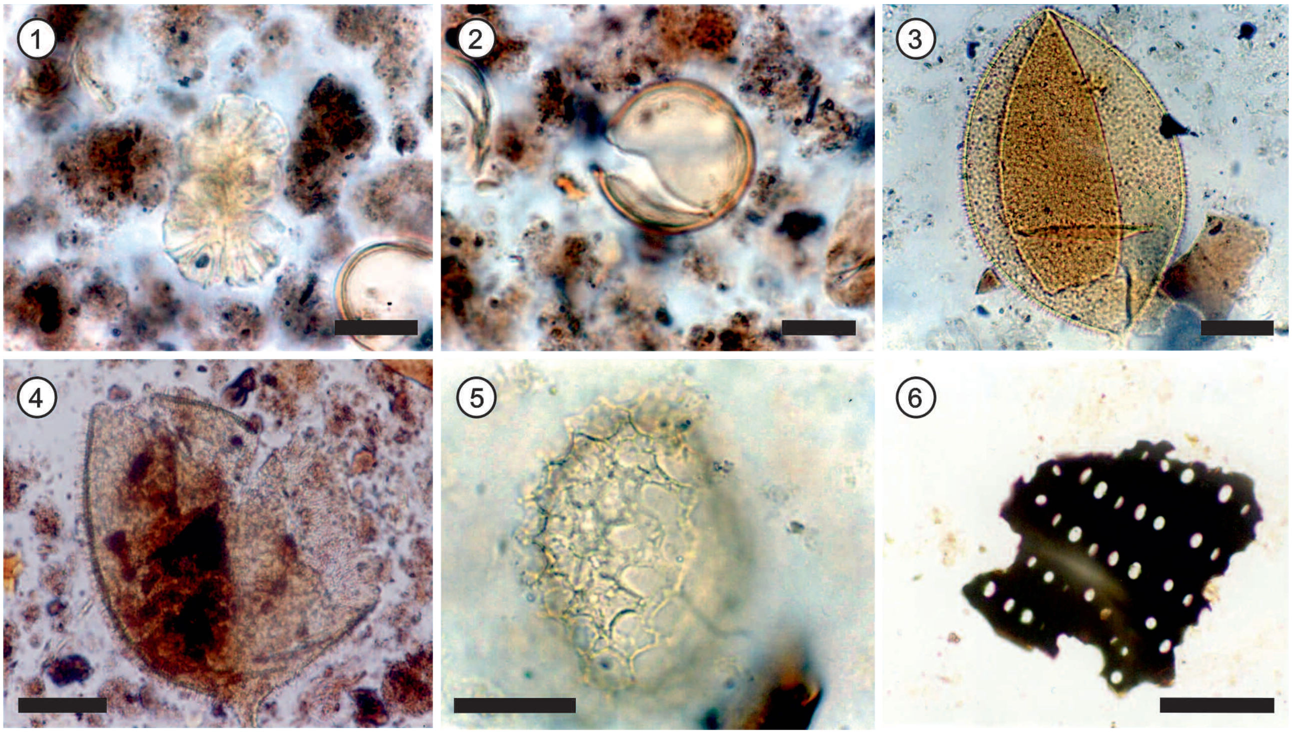

Figure 5. NPMs remains found in **QS-2c** Pollinic Subzone (Estancia Thomas profile)**. 1,** ***Botryococcus*** **sp**. **2,** ***Sigmopollis*** **sp**. **3** and **4,** Copepods eggs. **5,** Rotifers eggs. **6,** Tracheid. Scale bar= 50 μm, except 1, 2 and 6 scale bar= 20 μm.

zation in the Chascomús lagoon, from the beginning of the 18th century to the middle of the 19th century, based on evidence yielded by sedimentology, geochemistry and ostracods.

In the Estancia Thomas area, the stratigraphic sequence ends with 70 cm thick light gray sandy sediments, with net-erosive base on the preceding unit. This unit is interpreted as deposited by overflows at the modern mouth of the Quequén Salado River and is assigned to Chacra La Blanqueada Formation (Rabassa, 1989). In these sediments, at least one former palaeosurface was found, characterized by the presence of an edaphization level (Farinati and Zavala, 1995). The sequence ends with the present soil. Radiocarbon dating on the organic matter of the sediments at the top of this unit yielded a minimum age of 207 cal. yr BP.

QS-1 Pollen Zone (Grill, 2003), recorded in this unit, starts with three samples yielding only a presence of pollen grains, not enough to reconstruct the plant communities. The NPMs are represented by fungal spores types "B" and "J" (Romero and Fernández, 1981), *Pluricellaesporites* sp. and *Glomus* sp., among others, and by *Botryococcus* sp. and algae type 128 A/B (van Geel *et al.*, 1982/1983). Among these, *Glomus* sp. indicates active erosive processes, and *Botryococcus* sp. evidences arid conditions and oligotrophic environments (Guy-Ohlson, 1992; van Gell and Aptroot, 2006).

Towards the top of the unit (207 cal. yr BP), the two samples closest to the surface present an assemblage analogous to the one currently colonizing the dunes and interdunes depressions at the lower basin of the Quequén Salado (Grill and Lamberto, 2006), but with lower proportions of Poaceae. The anthropic influence of the natural plant communities is evidenced by Tamaricaceae, Brassicaceae (7%), *Eucalyptus* sp. and *Pinus* sp. Among the NPMs, Bryophytes (*Phaceros laevi* Proskauer, 1951) and Pteridophytes spores stand out, along with some fungal spores (*Glomus* sp.).

The human impact evidenced in the assemblages is similar to that recorded in other equivalent stratigraphic sequences from rivers and streams of the region (Borromei,

TABLE 4. Synthesis of the palaeoenvironmental and palaeoclimatic fluctuations registered at the lower basin of the Quequén Salado River, from multi-proxies analysis.

Age ◆ Cal. years BP (average)		Sedimentology (Farinati and Zavala, 1995; Grill et al., 2010)		Malacofauna (Farinati and Zavala, 1995)	Palynomorphs (Grill, 2003; Grill et al., 2010)	
					Vegetational palaeocommunities	Marine Palaeomicroplankton
Late Holocene/historical times	◆ 207	Modern soil			Herbaceous steppe with introduced pollen	
	◆ 389	Dense and compact silts			Few steppe elements Brassicaceae (50%)	
	◆ 690–832	Sandy loams			Psammophyte herbaceous steppe Poaceae (20%)	
	◆ 832	Clayey silts			Presence of pollen	
Middle Holocene	◆ 4603	Finings upwards sequence		**Heleobia australis** *and* Characeae's oogonia	Few steppe elements with arboreal extra-regional pollen	
					Presence of pollen	
	◆ 6,799				Gramineuos steppe	**Micrhystridium** *sp.*, **Micrhystridium balmei** *and* **Spiniferites** *sp.* (scarce specimens)
Early Holocene	◆ 8,173	Sedimentary facies of marine origin	Facies "C"	**Tagelus plebeius**	Halophyte steppe Chenopodiaceae (67%)	**Micrhystridium** *sp.*, **Cymatiosphaera polonica**, **Cymatiosphaera** *sp.*
			Facies "B"	**Ostrea spetra**, **Brachidontes rodriguezi**, **Tagelus plebeius**		
			Facies "A"		Presence of pollen	**Micrhystridium** *sp. and* **Cymatiosphaera** *sp.*
Pleistocene/Holocene transition		Palaeosoil (horizon A)			Halophyte steppe Chenopodiaceae (64%)	
LGM?		Sandstone with bioturbation			Sterile samples	

1995, 1998; Grill, 1995, 1997, among others).

The palaeoclimatic inferences for the base of the upper section of the Estancia Thomas Profile indicate adverse conditions for pollen preservation but favourable for the development of the previously mentioned NPMs (*Glomus* sp. and *Botryococcus* sp.). Such conditions might correlate to those inferred for the QS_1 Site (Little Ice Age?). Towards the top of the Estancia Thomas Profile, an establishment of subhumid/dry conditions, reminiscent of today climate, is inferred by the palynomorph assemblages.

CONCLUSIONS

The steppe communities recorded from the Late Pleistocene (LMG?) to present time confirm, as stated by Barreda *et al*. (2007), that the Argentinian flora of the studied geological lapse does not differ significantly from the modern flora. The variations observed in the proportions of the different pollen types and in the composition of the assemblages would be related to the movement of the Atlantic and Pacific anticyclones, to the variations of the west and east winds, and to sea level fluctuations.

For the Late Pleistocene (LGM?), when the sea level was lower than today, barren palynological samples illustrate adverse conditions for pollen preservation. These were associated with environments of extreme aeolian and arid conditions. The scarce populations of ostracods and diatoms ratified such inferences.

During the Late Pleistocene/Holocene transition, a brief episode of climatic stability, associated with a pedogenetic event, was inferred for the Estancia Thomas Profile sequence. The halophyte communities were similar to those currently colonizing the mudflats of Bahía Blanca Estuary (200 km south the study area). This type of vegetal cover remained in the area approximately until the Middle

Table 4. Continuation.

NPMs (Grill, 2003; Grill et al., *2010)*	*Ostracods and diatoms (Martínez and Gutiérrez Tellez, 1998)*		*Palaeoenvironments*	*Palaeoclimates*	*Sea-level curve (this paper)*
Bryophyte, Pteridophyte, fungi and algae spores			*Floodplain*	*Semiarid*	
				LIA	
Abundance algae and Bryophyte				**MCO*	
Abundance of fungi spores				*Semiarid*	
Corticeaceae, **Glomus** *sp.,* **Botryococcus** *sp.,* **Spyrogira** *sp. and crustacean eggs*	*Alternation of diatoms;* **Hyalodiscus laevis** *and* **Surirella striatula**		*Lagoon*	*Semiarid with wet and dry pulses*	
	Predominance of **Lymnocythere** *sp. and* **Surirella striatula, Campylodiscus clypeus** *like presence*				
Glomus *sp.,* **Botryococcus** *sp.*	*Predominance of* **Cytherura dimorphica, Leptocythere** *sp.,* **Perissocytherideae** *sp.,* **Semixestoleberis debueni, Actinoptychus splendens, A. senarius** *and* **Triceratium** *sp.*	*Shallow marine*	*"Mixed flat"*	*Semiarid with brief aridity pulses*	
			"Forshore"		
			Transgressive waste deposit		
			Coast	*Semiarid*	
	Scarce populations		*Eolian*	*Arid/extremely arid*	

Abundance of archeological and faunistic remains,* **Cavia aparea *(Grill* et al., *2010).*

Holocene. For this area, the sedimentology, malacofauna and microfossils (acritarchs, marine palaeomicroplankton, ostracods and diatoms) evidenced a sea level rise during the Early Holocene (8,173 cal. yr B.P.). Some NPMs indicated brief arid pulses in a regional context of semiarid conditions. This transgressive event ended with the establishment of a brackish lacustrine body towards the Middle Holocene. Between ~6,799 cal. yr BP and 5,603 cal. yr BP, the pollen assemblages, NPMs, ostracods and diatoms showed significant variability, thus evidencing an alternation between humid and dry pulses.

During the Late Holocene, ~1.000 yr. BP, it can be posited that the lower basin of the Quequén Salado saw the settlement of modern ecosystems (dunes and interdunes), with the sea and the river resembling their current position.

At the QS$_1$ Archaeological Site, two global climatic changes, the Medieval Climatic Optimum (823-690 cal. yr BP) and the Little Ice Age (389 cal. yr BP), were inferred on the basis of pollen and faunistic remains.

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VOLUMEN TEMÁTICO

ANÁLISIS E INTERPRETACIÓN DE REGISTROS PALINOLÓGICOS DE SUCESIONES ALUVIALES DE LA REGIÓN PAMPEANA: REVISIÓN E IMPLICANCIAS PARA LA RECONSTRUCCIÓN DE LA VEGETACIÓN Y EL CLIMA DURANTE EL PLEISTOCENO TARDÍO–HOLOCENO

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Resumen. En este trabajo se sintetizan y discuten los resultados de *ca.* 30 años de estudios palinológicos de depósitos aluviales del Pleistoceno Tardío–Holoceno de la región pampeana (RP). La mayor parte de las reconstrucciones de la vegetación para ese lapso han derivado del análisis polínico de depósitos aluviales, aunque en ciertos casos los resultados son controvertidos. La presente revisión muestra que el análisis palinológico de sucesiones aluviales es un recurso importante de información paleoambiental cuali y cuantitativa para la RP, pero también expone que no todas las secuencias polínicas publicadas son adecuadas para hacer reconstrucciones de la vegetación y el clima. Las principales causas de discrepancias entre los resultados han sido el escaso entendimiento sobre el transporte fluvial del polen, la preservación polínica y la tafonomía, y el control de las facies sedimentarias en las posibles modificaciones de los registros polínicos. Las causas de la alteración de los conjuntos polínicos, aunque relacionadas principalmente con repetidos ciclos de hidratación-desecación, degradación microbiana y posible control de facies, han sido escasamente discutidas en la mayoría de los trabajos. Esto señala la necesidad de realizar estudios sobre la preservación polínica diferencial y la cuantificación del polen transportado por los ríos, poniendo más atención en el conocimiento de los procesos tafonómicos para mejorar la interpretación de los registros palinológicos fósiles. A pesar de esto, los progresos realizados recientemente han permitido lograr reconstrucciones significativamente más precisas e informativas de la vegetación y del clima del pasado en la RP que lo que fue posible anteriormente.

Palabras clave. Palinología fluvial. Tafonomía. Preservación polínica. Argentina.

Abstract. ANALYSES AND INTERPRETATION OF PALYNOLOGICAL RECORDS FROM ALLUVIAL SEQUENCES OF THE PAMPAS REGION: REVIEW AND IMPLICATIONS FOR VEGETATION AND CLIMATE RECONSTRUCTION DURING THE LATE PLEISTOCENE–HOLOCENE. In this review the results of Late Pleistocene–Holocene palynological studies from alluvial deposits in the Pampean region (PR) performed over the last *ca.* 30 years have been synthesized and discussed. Most vegetation reconstructions for that period have been derived from pollen analysis of alluvial deposits, although in some cases the results are controversial. The present review shows that palynological analysis from alluvial sequences is an important resource of qualitative and quantitative paleoenvironmental information for the PR, but also states that not all published pollen records are suitable for vegetation and climate reconstructions. The main causes of discrepancies between the results are the limited understanding of pollen fluvial transport, pollen preservation and taphonomy, and sedimentary facies control that could have altered the pollen records. The causes of the alteration of the pollen assemblages, although mainly related to repeated wetting-drying cycles, microbial degradation and possible control of facies, have scarcely been discussed in most works. This points the need for studies on differential pollen preservation and quantification of pollen transported by river water, paying more attention to the knowledge of taphonomic processes to improve the interpretation of fossil palynological records. Even so, the progress achieved recently have made possible to obtain significantly more precise and informative reconstructions of past vegetation and climate in the PR than was possible earlier.

Key words. Fluvial palynology. Taphonomy. Pollen preservation. Argentina.

El análisis palinológico de sucesiones aluviales ha sido utilizado para reconstruir la historia de la vegetación y del clima durante el Cuaternario Tardío en varias áreas del Hemisferio Norte desde hace décadas. Los primeros trabajos se realizaron en la región semiárida del sudoeste de EEUU (*e.g.*, Martin, 1963; Mehringer, 1967; Mehringer *et al.*, 1967; Hall,

1977) y en el este de Rusia (*e.g.*, Grichuk, 1967 y referencias allí citadas).

En las últimas décadas el análisis palinológico de sucesiones aluviales se ha incrementado, especialmente en las Grandes Llanuras y el sudoeste de EEUU (Delcourt y Delcourt, 1980; Hall, 1981, 1985, 1989, 1995, 2010; Fall, 1987; Baker *et al.*, 2000; Work *et al.*, 2005), en el norte de China (*e.g.*, Xu *et al.*, 1996; Ma *et al.*, 2004) y en algunos países de Europa (*e.g.*, Bisernia y van Geel, 2005; Albert y Pokorný, 2012).

Los estudios pioneros en Argentina fueron realizados por D'Antoni *et al.* (1985) y Prieto (1989) en la región pampeana (RP). En los últimos 30 años numerosos investigadores han utilizado el análisis palinológico de sucesiones aluviales de esta región para reconstruir la vegetación e inferir las condiciones ambientales y climáticas, principalmente durante el Holoceno (Tab. 1; Fig. 1). En dos sucesiones aluviales (sitio 18 y 4, Fig. 1) se estudiaron únicamente los palinomorfos fúngicos (Borel *et al.*, 2001) y otros componentes orgánicos ácido-resistentes (Grill *et al.*, 2007),

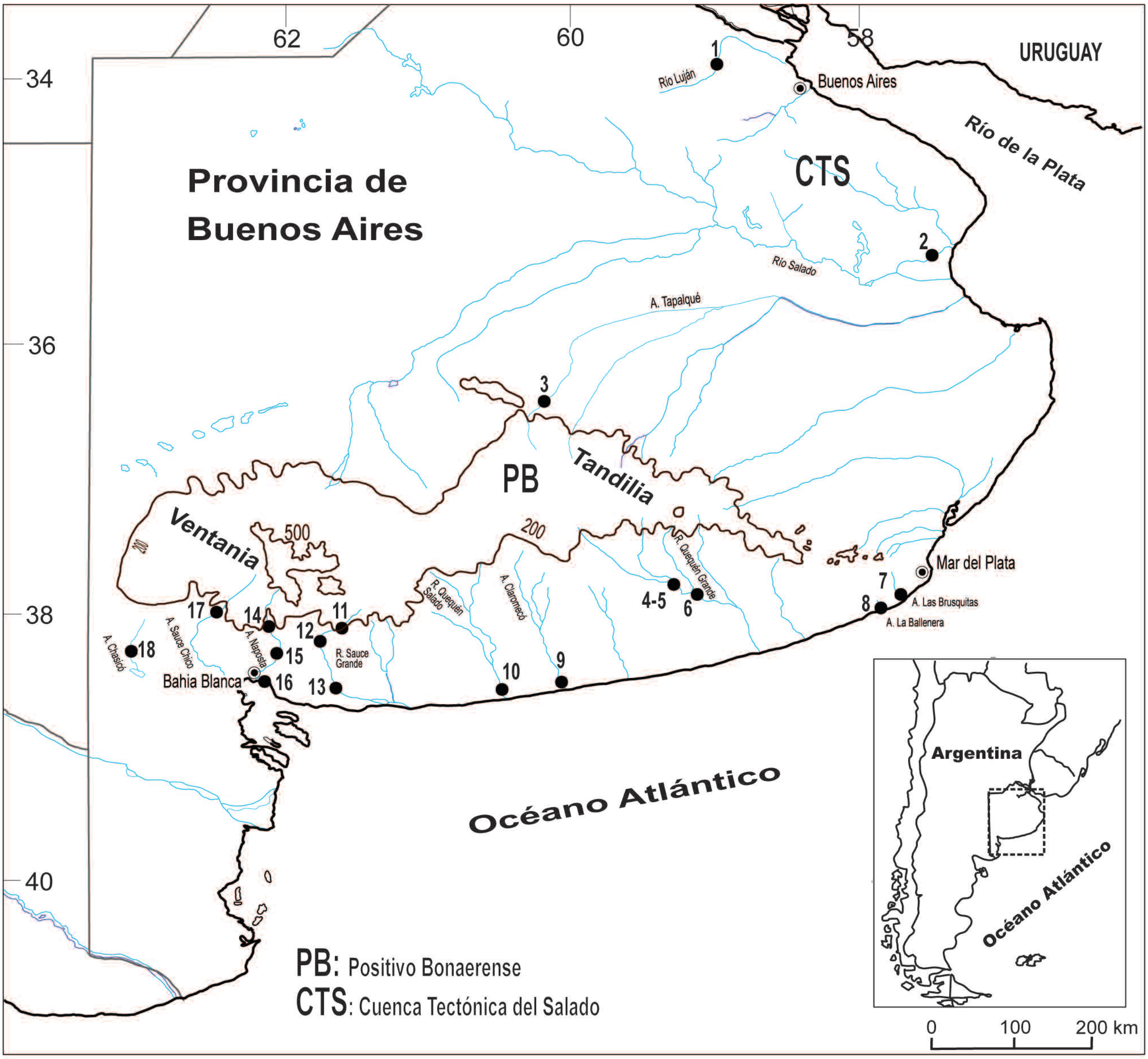

Figura 1. Mapa de ubicación de las sucesiones aluviales donde se realizaron los estudios palinológicos (ver referencias en Tabla 1).

TABLA 1 – Sucesiones aluviales de la región pampeana donde se han realizado análisis palinológicos.

Sitio	*Nombre*	*Ubicación lat. (S); long. (O)*	*Rango temporal*	*Referencias*
1	*Río Luján (Paso de la Tropa)*	*34° 34’; 59° 08’*	*Holoceno Tardío*	*Prieto* et al. *(2004)*
2	*Río Salado*	*35° 55’; 57° 53’*	*Holoceno Medio–Tardío*	*Vilanova y Prieto (2012)*
3	*Arroyo Tapalqué*[a] *(Empalme Querandíes)*	*37° 00’; 60° 07’*	*Holoceno Pleistoceno Tardío (incompleto)*	*Prieto (1989, 1996, 2000); Prieto y Quattrocchio (1993)*
4	*Río Quequén Grande (Paso Otero 5)*	*38° 12’; 59° 06’*	*Holoceno Pleistoceno Tardío*	*Grill* et al. *(2007)*
5	*Río Quequén Grande (Paso Otero 4)*	*38° 12’; 59° 06’*	*Holoceno Temprano–Medio Pleistoceno Tardío (incompleto)*	*Gutiérrez* et al. *(2011)*
6	*Río Quequén Grande (La Horqueta II)*	*38° 18’; 58° 49’*	*Holoceno (incompleto) Pleistoceno Tardío (incompleto)*	*Prieto (2000)*
7	*Arroyo Las Brusquitas*[b]	*38° 14’; 57° 46*	*Holoceno Medio–Tardío Pleistoceno Tardío (incompleto)*	*D’Antoni* et al. *(1985); Prieto* et al. *(2003); Vilanova* et al. *(2006)*
8	*Arroyo La Ballenera*	*38° 53’; 60° 32’*	*Holoceno Medio*	*Stutz* et al. *(1999); Borel (2007)*
9	*Río Quequén Salado (Estancia Thomas)*	*38° 19’; 57° 57’*	*Holoceno Medio–Tardío (incompleto)*	*Grill (2003)*
10	*Arroyo Claromecó*[c]	*38° 50’; 60° 05’*	*Holoceno Medio–Tardío*	*Vilanova* et al. *(2010); Prieto* et al. *(2014)*
11	*Río Sauce Grande (La Toma)*	*38° 17’; 61° 41’*	*Holoceno Tardío*	*Madrid y Politis (1991)*
12	*Río Sauce Grande (Terraza II)*	*38° 29’; 61° 47’*	*Holoceno (incompleto) Pleistoceno Tardío (?) (*)*	*Borromei (1995)*
13	*Río Sauce Grande (Balneario Saldungaray)*	*38° 40’; 61° 45’*	*Holoceno Medio–Tardío (incompleto)*	*Borromei (1998)*
14	*Arroyo Napostá Grande (García del Río)*	*38° 21’; 62° 20’*	*Holoceno Tardío (incompleto) Pleistoceno Tardío (?)(*)*	*Grill (1995)*
15	*Arroyo Napostá Grande (Chacra Santo Domingo)*	*38° 32’; 62° 03’*	*Holoceno Tardío (incompleto) Pleistoceno Tardío (?) (*)*	*Grill (1997)*
16	*Arroyo Napostá Grande (Grünbein)*	*38° 46’; 62° 15’*	*Holoceno Medio–Tardío (incompleto)*	*Quattrocchio* et al. *(1998)*
17	*Arroyo Sauce Chico*	*38° 05’, 62° 16’*	*Holoceno Medio–Tardío*	*Prieto (1989, 1996); Prieto y Quattrocchio (1993); Tonello y Prieto (2010)*
18	*Arroyo Chasicó*	*38° 24’; 62° 51’*	*Holoceno*	*Borel* et al. *(2001)*

Incompleto: numerosas muestras estériles y/o presencia de algunos granos de polen o solo algunos niveles con polen. (*) Sin control cronológico.[a] *Tres secuencias en la misma localidad (Prieto, 1989, 2000);* [b] *Dos secuencias en la misma localidad (Vilanova* et al.*, 2006)* [c] *Cuatro secuencias en la misma localidad (Vilanova* et al.*, 2010)* porque la mayoría de las muestras eran polínicamente estériles. Por otra parte, Prieto y Quattrocchio (1993) realizaron la única descripción y análisis de las briofitas y pteridofitas del Holoceno de la RP a partir de varias secuencias polínicas, algunas de las cuales provenían de depósitos aluviales (sitios 3 y 17, Fig. 1). En ese estudio se enfatizó que la información paleoambiental que brindaron las esporas de briofitas era de carácter local y se hipotetizó sobre la representación extra local y las posibles rutas migratorias de las pteridofitas durante el Holoceno.

Recientemente Rojo *et al.* (2012) iniciaron el análisis polínico de sucesiones aluviales del Holoceno Medio y Tardío en las regiones áridas-semiáridas del oeste de Argentina. A partir de esos análisis infirieron cambios locales de las comunidades vegetales de la llanura de inundación en respuesta a la dinámica fluvial del Arroyo La Estacada (33° S) durante ese tiempo.

La mayoría de los estudios palinológicos de depósitos aluviales de la RP provienen de afloramientos en los cursos colectores principales del Positivo Bonaerense y unos pocos de la Cuenca Tectónica del Salado (Fig. 1). Representan el material detrítico transportado y depositado por una corriente de agua principalmente en la llanura de inundación, en cuerpos de agua de tamaños variables en el valle y en la desembocadura, donde formaron ambientes estuáricos. Las sucesiones son estratigráficamente similares y muestran secciones semejantes como resultado de procesos sedimentarios discontinuos, indicados por superficies de erosión y desarrollo de suelos que señalan fases de relativa estabilidad (Fig. 2). Estas sucesiones representan el relleno sedimentario de los valles actuales, constituido principalmente por conglomerados y arenas basales a las que continúan depósitos arenosos y pelíticos y loess retrabajado por procesos fluviales del Pleistoceno Tardío (*ca.* 40.000–10.000 ^{14}C años AP). Para el Holoceno está representado por facies fluvio-lacustres, palustres y estuáricas que se acumularon en las áreas deprimidas de la paleotopografía preexistente, que presentan una geometría lenticular; y facies eólicas (Fig. 3). Durante el Holoceno Temprano y Medio dominó la sedimentación bioclástica (diatomitas o sedimentos diatomáceos y niveles con concentración de moluscos dulceacuícolas o estuarinos), durante el Holoceno Tardío dominó la sedimentación eólica y recientemente la aluvial (*e.g.*, Fidalgo *et al.*, 1973; Rabassa, 1989; Zavala y Quattrocchio, 2001; Prieto *et al.*, 2004; Zárate, 2005; Fucks *et al.*, 2010). La excavación de los cauces de los ríos y arroyos habría ocurrido con posterioridad a *ca.* 3000 años ^{14}C AP (Zárate *et al.*, 2000; Vilanova *et al.*, 2010) lo cual permitió la preservación y exposición fuera del área de incisión de un amplio conjunto de depósitos pre-incisión de varias edades que registran una historia detallada de los episodios de agradación durante el Pleistoceno Tardío–Holoceno.

Fall (1987) sugirió que el polen de depósitos aluviales no era confiable para la reconstrucción de paleoambientes. Sin embargo, la mayoría de los autores mencionados al inicio de esta revisión están en desacuerdo y reconocen que es una herramienta adecuada para realizar reconstrucciones de la vegetación local y regional y del clima del pasado; pero recomiendan que para que las interpretaciones sean más ajustadas se consideren (1) las facies sedimentarias y la configuración geomorfológica de los depósitos aluviales (Hall, 1989; Xu *et al.*, 1996; Work *et al.*, 2005) y (2) se entienda el papel de la tafonomía en la supuesta modificación de los conjuntos polínicos de estos depósitos (Brush y Brush, 1972; Fall, 1987; Albert y Pokorný, 2012).

Los estudios combinados de estratigrafía y análisis palinológico han contribuido a mejorar, precisar y profundizar la comprensión de los cambios observados en los ambientes aluviales, la vegetación y las condiciones ambientales y climáticas en la RP. Sin embargo, en ciertos casos los resultados son controvertidos (Prieto *et al.*, 2009) y en consecuencia plantean varias cuestiones para discutir sobre el análisis palinológico de sucesiones aluviales en esta región. Por esta razón, en este trabajo se han sintetizado los resul-

Figura 2. Ejemplos de sucesiones aluviales en la región pampeana. **1,** Arroyo Claromecó (sitio 10). **2,** Río Quequén Salado (sitio 9). **3,** Arroyo Las Brusquitas (sitio 7). **4,** Río Quequén Salado. **5,** Río Salado (sitio 2). **6,** Arroyo Tapalqué (sitio 3). **7,** Arroyo Sauce Chico (sitio 17). Fotografías: A.R. Prieto. Para detalles ver las referencias citadas en la Tabla 1.


1


2


3
1 m


4
1 m


5
0,50 m


6
1 m


7

tados de *ca*. 30 años de estudios con los siguientes objetivos: (1) analizar el transporte fluvial, los procesos tafonómicos y el control de las facies sedimentarias en las posibles modificaciones de los registros polínicos de los depósitos aluviales; (2) evaluar la confiabilidad del contenido polínico de estos depósitos; y (3) discutir las potencialidades y limitaciones de los registros palinológicos de depósitos aluviales en los estudios de reconstrucción de la vegetación y del clima de la RP.

En este trabajo se utiliza el término "polínico" cuando el análisis incluyó el estudio del polen y de las esporas de pteridofitas y briofitas (Seppä, 2013) y el término "palinológico" cuando el estudio incluyó además a los palinomorfos no polínicos (van Geel, 2001), los dinoquistes y los acritarcos. La nomenclatura de las plantas vasculares sigue el catálogo del Instituto de Botánica Darwinion de Argentina (http://www.darwin.edu.ar) y el del *Missouri Botanical Garden* (http://www.tropicos.org/).

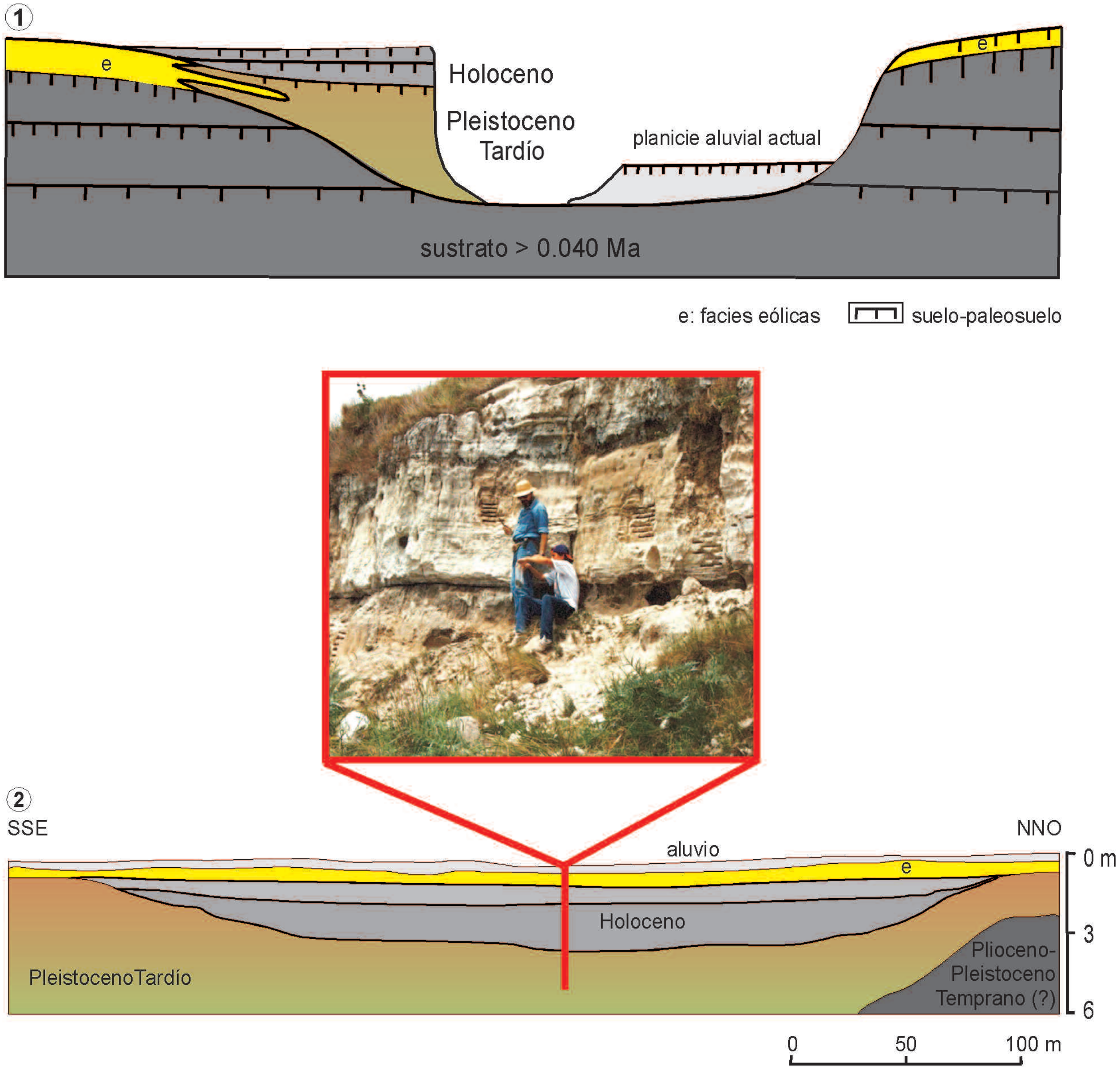

Figura 3. 1, Esquema simplificado de un valle fluvial en el Positivo Bonaerense (modificado de Zárate, 2005). **2,** Geometría del sitio La Horqueta II (modificado de Zárate *et al*., 1998) indicado en rojo y en la fotografía la sección estratigráfica estudiada.

TRANSPORTE FLUVIAL DEL POLEN

El polen transportado fluvialmente es una importante fuente de palinomorfos contenidos en los depósitos aluviales y los palinólogos han tenido diferentes opiniones sobre el polen aluvial. Por tal motivo, han examinado el polen suspendido en el agua en numerosos ríos y arroyos (*e.g.*, Catto, 1985; Chmura y Liu, 1990; Traverse, 1992; Smirnov *et al.*, 1996; Xu *et al.*, 1996; Chmura *et al.*, 1999; Brown *et al.*, 2007, 2008) y el incluido en muestras de sedimento superficial (*e.g.*, Grichuk, 1967; Solomon *et al.*, 1982; Fall, 1987; Xu *et al.*, 1996; Moss *et al.*, 2005; Rojo *et al.*, 2012), para evaluar las fuentes fluviales del polen. Estos últimos estudios se han realizado en diferentes ubicaciones dentro del ambiente fluvial como la llanura de inundación, las barras, el lecho, los albardones e incluso en la llanura aluvial fuera del río, tanto en grandes ríos que atraviesan diferentes zonas geográficas como en tributarios localizados dentro de una única zona.

Algunos estudios han mostrado que la composición taxonómica de los conjuntos polínicos transportados por el agua de los ríos no tendría el mismo efecto sobre aquellos involucrados en el transporte por el viento, particularmente sobre el efecto que el transporte por el agua tendría en la clasificación del polen. Brown (1985), Catto (1985), Fall (1987) y Xu *et al.* (1996) han argumentado que el transporte fluvial tiende a clasificar hidráulicamente a los granos de polen por tamaño, concentrando preferentemente a unos como componentes de la fracción arena y a otros con la fracción limo-arcilla. Estos hallazgos son consistentes en general con los modelos experimentales de transporte de polen en un canal artificial y, si bien el tamaño es el factor más importante en la clasificación, también están involucradas la forma y/o la densidad de los granos de polen (Brush y Brush, 1972; Holmes, 1990). Contrariamente, Solomon *et al.* (1982), Hall (1989), Chmura y Liu (1990), Campbell y Chmura (1994), Smirnov *et al.* (1996) y Moss *et al.* (2005), han concluido que la clasificación de los granos de polen por el transporte fluvial no es un factor significativo, que los conjuntos polínicos son independientes de la textura sedimentaria y que no es esperable que el transporte fluvial provoque distorsiones de los conjuntos polínicos en los sedimentos. Por lo tanto, los granos de polen transportados fluvialmente reflejarían fielmente a las comunidades vegetales y podrían utilizarse en la reconstrucción de la vegetación y del clima del pasado.

Estas conclusiones no son extrapolables de manera directa a todas las regiones y depósitos aluviales e incluso las interpretaciones de los registros polínicos fósiles a partir de estos estudios actualísticos difieren para un mismo ambiente (*e.g.*, región semiárida del sudoeste de EEUU: Fall, 1987; Hall, 1989). Este tipo de estudios no se ha realizado en la RP y si bien algunos de los resultados pueden utilizarse para la interpretación de los conjuntos polínicos fósiles provenientes de los depósitos aluviales, también es esperable diferencias debido a que las regiones donde se obtuvieron esas conclusiones tienen comunidades vegetales y condiciones climáticas diferentes a la RP. Sin embargo, este conocimiento ha sido usualmente descuidado en los estudios de las secuencias polínicas fósiles de esta región. Solamente en el registro palinológico Arroyo Sauce Chico, ubicado en el curso medio del arroyo homónimo (sitio 17, Fig. 1), se explicó la presencia de las pteridofitas *Cheilanthes*/*Pellaea* spp., *Notholaena squamosa* (Gillies y Hook. ex Grev.) Hook. y Baker, *Anemia tomentosa* (Sav.) Swartz, *Doryopteris* sp. y *Polypodium* sp. como resultado del transporte fluvial de estas esporas desde la región serrana de Ventania (Fig. 1), donde nace el arroyo y se desarrollan esas plantas (Prieto y Quattrocchio, 1993). Esto sugiere la posibilidad de que el agua transporte también polen desde las cabeceras, el cual contribuiría al conjunto polínico de los sedimentos aluviales aguas abajo.

Por otra parte, el transporte y la suspensión diferencial explicarían la heterogeneidad de los espectros polínicos provenientes de los mismos depósitos aluviales del Holoceno del Arroyo Napostá Grande (Grill, 1995, 1997; sitios 14 y 15, Tab. 1), en lugar de atribuirle una causa climática. La heterogeneidad está sugerida por señales polínicas diferentes y tendencias particulares en cada registro y ha dificultado la comparación entre las secuencias polínicas y la interpretación de los cambios de la vegetación a escala local como regional. Además, debería tenerse en cuenta un posible control de facies para explicar la heterogeneidad de cada registro, los cuales pueden diferir significativamente con diferentes facies (Xu *et al.*, 1996). Este control no ha sido contemplado, aun cuando la variabilidad facial es considerable en esas sucesiones (Quattrocchio *et al.*, 2008).

En los estudios actualísticos el polen de Poaceae fue asociado con el tamaño limo y correlacionado con ambientes de baja energía, y el de Cyperaceae y Chenopodiaceae con el tamaño arena y vinculados con ambientes de alta energía (*e.g.*, Brown, 1985; Catto, 1985; Fall, 1987). Por el contrario, en algunas secuencias de la RP el polen de Cyperaceae se presenta con las mayores frecuencias y concentraciones en los limos orgánicos (*e.g.*, Stutz *et al.*, 1999; Vilanova *et al.*, 2010) en una relación inversa a la obtenida en los estudios actualísticos. En general, la selección hidráulica por tamaños no es evidente en las secuencias polínicas de la RP, posiblemente porque el rango de tamaños de los granos de polen es equivalente al limo mediano hasta arena muy fina, litologías predominantes en los depósitos aluviales estudiados.

El resultado del transporte fluvial del polen debería ser considerado cuidadosamente en la reconstrucción de la vegetación. La influencia que el mismo puede tener sobre la representación polínica aún no está completamente entendida, en particular en lo referente a la forma en que este transporte afecta a la depositación y preservación del polen y, por lo tanto, a la representación polínica en un registro fósil (Moss *et al.*, 2005).

PRESERVACIÓN POLÍNICA Y TAFONOMÍA

Aunque la preservación del polen es un factor importante que afecta la correcta interpretación de un espectro polínico (*e.g.*, Bryant y Holloway, 1983; Campbell, 1991; Bunting y Tipping, 2000; Tipping, 2000), ha sido frecuentemente ignorada en las investigaciones de depósitos aluviales de la RP. Sin embargo, casi todos los conjuntos polínicos de las sucesiones aluviales involucran aspectos de la preservación del polen en cierta medida. La preservación polínica depende de muchos factores complejos que podrían agruparse en tres categorías (Bryant y Holloway, 1983): (1) las características intrínsecas del polen, tales como la composición química de la pared, el tamaño del grano y la estructura y escultura de la exina (Havinga, 1964, 1967, 1984); (2) los factores ambientales como la oxidación (pH y Eh) (Dimbleby, 1957; Tschudy, 1969; Bryant *et al.*, 1994; Twiddle y Bunting, 2010), la temperatura y humedad fluctuantes (Bryant y Holloway, 1983; Campbell y Campbell, 1994), la acción de hongos y bacterias (Havinga, 1970; Elsik, 1971) y la (bio) química (Havinga, 1964) y (3) la degradación mecánica (abrasión) (Catto, 1985; Fall, 1987), aunque en un experimento de laboratorio se encontró que la evidencia de daños causados por factores mecánicos era escasa (Campbell, 1991).

En varios trabajos de la RP se ha reconocido que la mala preservación y la destrucción diferencial del polen es recurrente en las sucesiones aluviales (*e.g.*, Prieto, 2000; Borel *et al.*, 2001; Prieto *et al.*, 2004; Grill *et al.*, 2007; Quattrocchio *et al.*, 2008; Vilanova *et al.*, 2010), sin embargo, los posibles factores tafonómicos que las han causado han sido escasamente discutidos. Prieto (2000) explicó la preservación diferencial en algunas muestras del sitio 3 (Fig. 1), que presentaban hasta el 70% de los granos de polen deteriorados, como producto de la actividad microbiana en función del patrón de alteración que presentaba la pared de los granos (Havinga, 1970, 1984). Esas muestras no fueron consideradas en los análisis porque el conjunto polínico no era confiable. La actividad microbiana también fue propuesta por Prieto *et al.* (2004) como el factor más probable responsable de la degradación polínica en una secuencia del Río Luján (sitio 1, Fig. 1) en lugar de un pH alto, basado en que la falta de correlación entre los porcentajes de CO_3Ca, los porcentajes de polen degradado y los valores de concentración polínica total, no sustentaban una relación con un ambiente alcalino. Una conclusión similar fue observada por Bryant *et al.* (1994) para muestras fósiles del sudoeste norteamericano.

Vilanova *et al.* (2006) han relacionado la mala preservación de los palinomorfos en algunos niveles ente *ca.* 3900 y 3000 ^{14}C años AP en el Arroyo Las Brusquitas (sitio 7, Fig. 1) con la desecación periódica y el retrabajo asociados a una zona supralitoral.

Grill *et al.* (2007) realizaron una clasificación de las clases de deterioro de la materia orgánica palinológica y de los posibles procesos responsables que eliminaron casi por completo el polen de las muestras de sedimento de una sucesión aluvial (sitio 4, Fig. 1). Estos autores atribuyeron como la causa principal de la destrucción del polen a un pH alto, pero también señalaron a otros factores como la oxidación química y bioquímica y el daño mecánico, sin explicar en qué casos y cómo afectaron al polen. Debido al escaso contenido de polen preservado, el análisis palinofacial que realizaron está sesgado y la interpretación no reflejaría de manera representativa a la vegetación local ni regional durante el lapso considerado, dando lugar a interpretaciones paleoecológicas erróneas.

La ausencia casi total de polen en muchos de los depósitos aluviales del Pleistoceno Tardío y el Holoceno Temprano podría explicarse por el descenso del nivel freático y repetidos ciclos de hidratación-desecación como consecuencia de la excavación de los cauces y las fluctuaciones del nivel freático, respectivamente (*e.g.*, Vilanova *et al.*, 2010). Hasta el momento de la disección, ocurrida con posterioridad a *ca.* 3000 ^{14}C años AP, el nivel freático era alto y en consecuencia es factible conjeturar que durante ese lapso el sustrato estuvo en condiciones de saturación y por lo tanto reductoras (bajo Eh). Con posterioridad a la incisión, el depósito sedimentario que contiene al polen sin-depositacional pasó a ser un sustrato aireado en un ambiente oxidante y con cambios en el Eh (Tonello *et al.*, 2002). Un Eh alto ocasiona un deterioro químico de la exina y una destrucción diferencial o total de los granos de polen (Tschudy, 1969), así como los ciclos repetidos de hidratación-desecación son una de las causas principales de la rápida degradación del polen (Holloway, 1989; Campbell y Campbell, 1994). Por lo tanto, la ausencia o mala preservación sería el resultado de alteraciones post-depositacionales, como se ha registrado en otros depósitos aluviales (*e.g.*, Hall, 1977, 1995) aunque no se puede descartar un deterioro sin-depositacional. Estas explicaciones resultan más parsimoniosas que aquellas que atribuyeron la ausencia de polen en los registros del Pleistoceno Tardío a condiciones extremadamente áridas (Grill, 1995; Quattrocchio *et al.*, 2008), a una cobertura vegetal reducida por condiciones ambientales severas (Grill, 1995) y/o a la ausencia de cobertura vegetal (Grill *et al.*, 2007), en contradicción con los numerosos resultados palinológicos obtenidos en depósitos de zonas áridas (*e.g.*, Horowitz, 1992 y referencias allí citadas).

Aunque los niveles freáticos pueden haber estado muy bajos en los valles aluviales durante el Holoceno Tardío, los depósitos también pueden haber tenido una larga historia de percolación de agua. A estos procesos post-depositacionales que pueden alterar los conjuntos polínicos, que generalmente involucran la destrucción y la pérdida por oxidación del polen, se le deben añadir los procesos de meteorización y formación de suelos, ocurridos en varios momentos del Holoceno (*e.g.*, Zárate, 2005). La génesis de los suelos ocurrió durante y con posterioridad a los procesos de sedimentación (*e.g.*, Zárate *et al.*, 2000). La superficie enterrada de esos paleosuelos suele estar indicada en los registros polínicos por un incremento de la concentración polínica total, una disminución de los granos deteriorados y un aumento de *Glomus*, un hongo micorriza de los suelos (*e.g.*, Dimbleby, 1985; Vilanova *et al.*, 2010).

Los procesos tafonómicos son evidentes en algunas secuencias polínicas del Holoceno, las que presentan numerosos niveles estériles y/o con escasos granos de polen (indicados en los diagramas polínicos con el término "presencia" *e.g.*, Grill, 1995, 2003; Borromei, 1998). Estos resultados sugieren que ha existido una eliminación diferencial de ciertos tipos polínicos y en consecuencia se ha incrementado la importancia aparente de los tipos más resistentes. De esta forma, con el aumento del deterioro se introduce un sesgo en favor de aquellos tipos polínicos que son más fáciles de reconocer por el analista, como por ejemplo Chenopodiaceae, Brassicaceae y Asteraceae, como se observa en varias de las secuencias analizadas.

Modificaciones y alteraciones de los espectros palinológicos de depósitos aluviales de la región pampeana: una explicación posible a partir de un caso de estudio

Para ejemplificar las posibles modificaciones y alteraciones que podrían haber afectado a los espectros palinológicos de los depósitos aluviales de la RP, se presenta como caso de estudio los análisis palinológicos realizados en tres afloramientos del Río Quequén Grande (Fig. 1) en un tramo de 20 km. Se discuten las posibles causas de la mala preservación y/o ausencia de polen en relación con procesos post y sin-depositacionales, el transporte fluvial y el control de facies.

El primero de los análisis se realizó en La Horqueta II (sitio 6, Tab. 1) a partir de una sección en la margen derecha del mencionado río, representativa del registro aluvial del centro-sur de la RP (Zárate *et al.*, 2000) que abarcó desde el Pleistoceno Tardío (*ca.* 19.000–10.000 ^{14}C años AP) hasta la actualidad (Prieto, 2000). La sección datada entre 10.000 y *ca.* 3000 ^{14}C años AP es una diatomita que presenta una geometría lenticular y subyace a un depósito de origen eólico modificado por pedogénesis y enterrado por aluvio actual (Fig. 2). Los únicos conjuntos polínicos se recuperaron de siete niveles de la base de la diatomita (10.270–9000 ^{14}C años AP) y en dos del Pleistoceno (Prieto, 2000). Los espectros están dominados por polen de Brassicaceae, generalmente formando agregados (masas cohesivas de dos o más granos de polen del mismo taxón). Se interpretó que la sobrerrepresentación de este taxón fue originada por una rápida depositación local en relación con un ambiente disturbado, en lugar de un registro de preservación polínica diferencial (Prieto, 2000). Los demás niveles fueron estériles o solo se recuperaron escasos granos de polen, algunos mal preservados, los que no fueron utilizados para realizar reconstrucciones de la vegetación, ya que las sumas polínicas no eran estadísticamente representativas y la confiabilidad del registro estaría fuertemente cuestionada. Bajas concentraciones y mala preservación polínica también se han obtenido en niveles de diatomitas en diferentes sitios de Nuevo México y Texas, las que fueron atribuidas a procesos post-depositacionales (Hall, 1995).

La segunda sección está localizada en Paso Otero 5 (sitio 4, Tab. 1), 20 km aguas arriba y abarcó desde el final del Pleistoceno Tardío (> 10.440 ^{14}C años AP) hasta la actualidad (Grill *et al.*, 2007). Se trata de la misma sucesión aluvial identificada aguas abajo por Zárate *et al.* (1998, 2000) con algunas diferencias faciales (Johnson *et al.*, 2012). Prácticamente todas las muestras fueron polínicamente estériles o contenían escasos granos de polen para realizar recuentos y estaban dominadas por esporas de hongos (Grill *et al.*, 2007), indicando que habría ocurrido desde una preservación diferencial hasta la destrucción total del polen.

La tercera sección está ubicada 2 km aguas abajo de la anterior en Paso Otero 4 (sitio 5, Tab. 1). Ambos sitios forman parte de la localidad arqueológica homónima y los depósitos aluviales son semejantes. La secuencia polínica abarcó el lapso 10.500–2280 ^{14}C años AP y solo presenta escasas muestras estériles en la base del Holoceno (Gutiérrez *et al.*, 2011). Los espectros polínicos están dominados por Asteraceae, Brassicaceae y Poaceae acompañados por Chenopodiaceae y Apiaceae, todos en proporciones altamente variables. Brassicaceae exhibe proporciones mayores al 50% en varios niveles, entre *ca.* 6500 y 4500 ^{14}C años AP y Apiaceae alcanza hasta 58 y 65% en dos niveles datados en 8913 ± 49 y 4561 ± 41 ^{14}C años AP, respectivamente, y se presentan en agregados. La sobrerrepresentación de ambos fue relacionada con actividades humanas, sin embargo resultaría de una depositación local. Posiblemente el polen provendría de plantas acuáticas flotantes, donde Brassicaceae representaría a plantas semejantes al berro (*Nasturtium* sp.) (Vilanova *et al.*, 2010) y Apiaceae a *Hydrocotyle* sp., desarrolladas en ambientes de aguas someras, vegetados y con baja o nula velocidad de corriente como lo sugieren el polen de otras hidrofitas, las diatomeas, los fitolitos y los palinomorfos no polínicos (Gutiérrez *et al.*, 2011).

La disparidad en los resultados polínicos entre los tres registros no fue discutida en este último trabajo, aun cuando todos los registros provienen de los mismos depósitos aluviales y están ubicados muy próximos unos con otros. La preservación polínica diferencial y un control de facies, principalmente para las sucesiones del Holoceno son evidentes.

Según Johnson *et al.* (2012) existen algunas diferencias depositacionales entre las áreas de Paso Otero y La Horqueta que indican facies diferentes, con una sedimentación episódica y precipitación de carbonatos en la primera y aguas más o menos estancadas y depositación de diatomeas en la segunda. Estas diferencias también se reflejan en los estudios diatomológicos que sugieren que en La Horqueta II (Zárate *et al.*, 1998) los cuerpos de agua dulce-salobre fueron más profundos y menos vegetados que en Paso Otero 5 (Gutiérrez *et al.*, 2011). Probablemente, un cambio en el pH como respuesta a un aumento en el contenido de carbonatos, habría cambiado la química del agua favoreciendo la preservación de huesos en el primer sitio y la formación de diatomita en el segundo (Johnson *et al.*, 2012). Sin embargo, esto no explicaría totalmente las diferencias en la preservación polínica entre unas y otras secuencias.

La presencia de carbonato en las sucesiones aluviales durante el Holoceno Medio podría reflejar altas tasas de evaporación con la consecuente pérdida de CO_2 debido a un incremento de la temperatura del agua superficial, o una reducción de las precipitaciones que originaría un enriquecimiento post-depositacional del carbonato (Prieto *et al.*, 2004). Ambos casos tendrían su contraparte en cambios del nivel freático que ocasionarían ciclos de hidratación-dese-

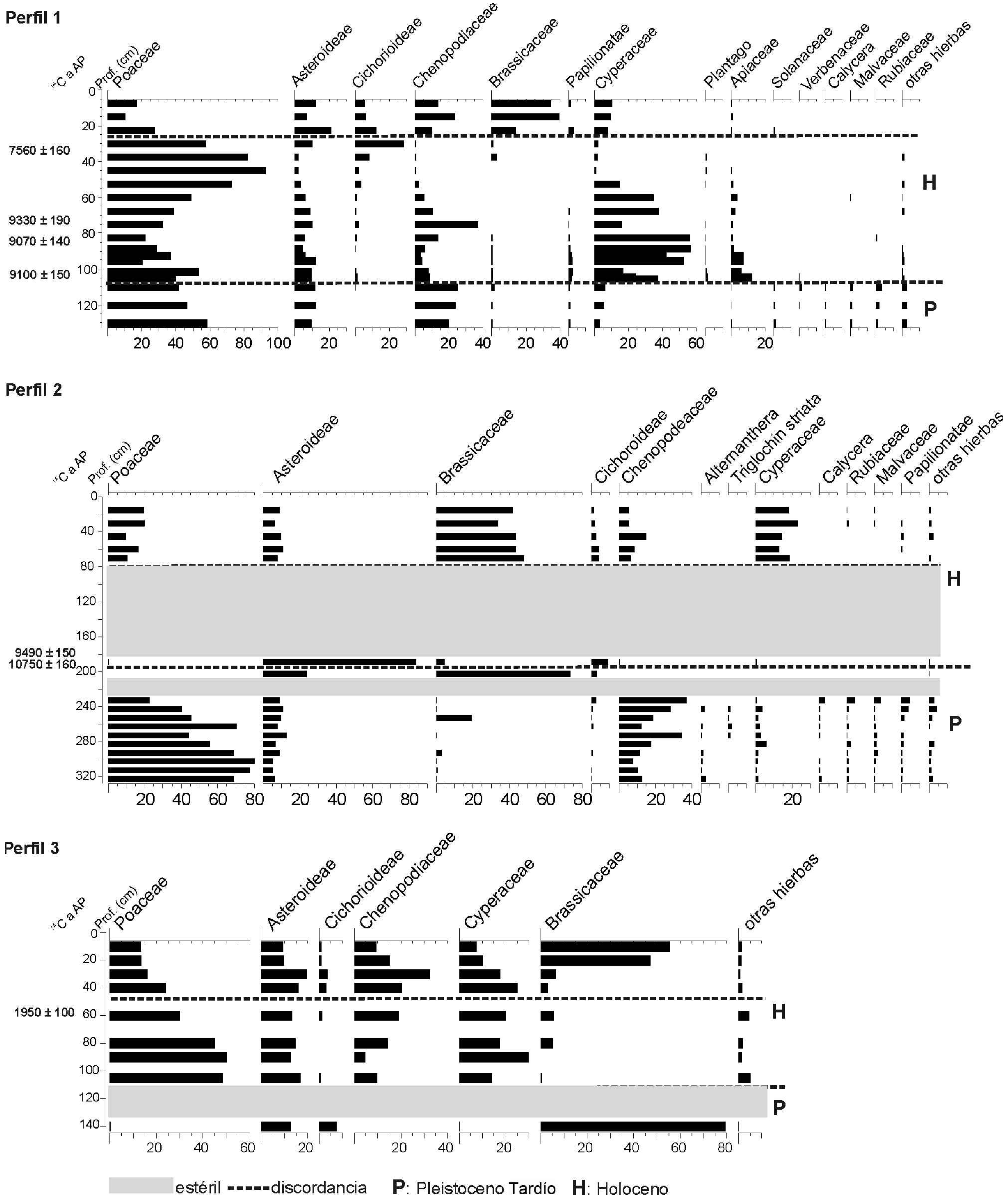

Figura 4. Diagramas polínicos en porcentajes de tres secciones estratigráficas en Empalme Querandíes, Arroyo Tapalqué (sitio 3, Fig. 1). Las secuencias se muestrearon en una sección transversal de 14 m (modificado de Prieto, 1989; 2000).

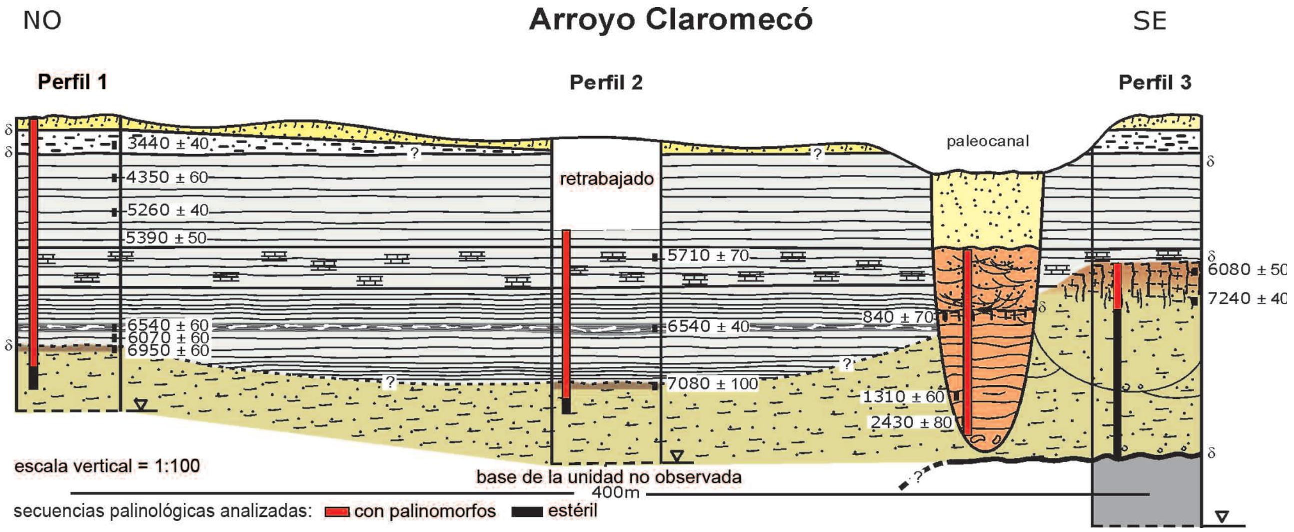

Figura 5. Sección general transversal de la estratigrafía del Pleistoceno Tardío-Holoceno del Arroyo Claromecó (sitio 10, Fig. 1) (modificado de Vilanova *et al.*, 2010).

cación que podrían degradar la pared de los granos y causar la destrucción del polen (Bryant y Holloway, 1983; Campbell y Campbell, 1994). Si los depósitos pueden retener suficiente humedad durante esos ciclos, podrían prevenir la desecación completa y los efectos de la hidratación-desecación sobre el polen podrían no ser tan severos (Bryant *et al.*, 1994) y esto explicaría la existencia de niveles con y sin polen.

Por otra parte, es notable que la secuencia que tiene el registro polínico con buena preservación (Paso Otero 4) sea la misma donde se han preservado huesos, sugiriendo que un pH alto no es necesariamente la principal causa de la destrucción del polen, como fue propuesto por Grill *et al.* (2007). Además, la diatomita puede haber tenido una larga historia de percolación de agua, a diferencia de los otros depósitos más arcillosos. En consecuencia, los ciclos de hidratación-desecación serían la principal causa para explicar la preservación diferencial del polen.

Es necesario resaltar que las secuencias palinológicas Paso Otero 4 y 5 (Tab. 1), separadas por 2 km y provenientes de la misma sucesión aluvial, muestran diferencias notables, que deberían tenerse en cuenta en la selección de secciones estratigráficas de depósitos aluviales para realizar estudios palinológico en futuros trabajos. El conocimiento de la geometría del cuerpo sedimentario y de la variabilidad facial de los depósitos aluviales permitirá seleccionar varios perfiles estratigráficos a lo largo de una sucesión aluvial. Los análisis palinológicos de estas sucesiones brindarán una información espacio-temporal más ajustada y confiable para realizar reconstrucciones de la vegetación y el ambiente del pasado, como lo ejemplifican los trabajos de Prieto (1989, 2000) y Vilanova *et al.* (2010) (Figs. 4, 5 y 6).

POTENCIALIDADES Y LIMITACIONES DE LOS REGISTROS PALINOLÓGICOS DE DEPÓSITOS ALUVIALES EN LOS ESTUDIOS DE RECONSTRUCCIÓN DE LA VEGETACIÓN Y EL CLIMA EN LA REGIÓN PAMPEANA

Reconstrucción de la vegetación

La mayor parte de las reconstrucciones de la vegetación de la RP para el Pleistoceno Tardío–Holoceno han derivado del análisis polínico de sucesiones aluviales. La introducción de técnicas numéricas multivariadas aplicadas a los datos de polen y vegetación actual de esta región han ayudado a los palinólogos a entender la relación entre el polen y las comunidades de plantas (*e.g.*, Stutz y Prieto, 2003; Tonello y Prieto, 2003, 2008; Vilanova y Prieto, 2012) y a ajustar las interpretaciones de los conjuntos polínicos fósiles de las sucesiones aluviales (Prieto, 1996, 2000; Vilanova *et al.*, 2006; Vilanova y Prieto, 2012). Sin embargo, en la mayoría de los trabajos las interpretaciones se han basado principalmente

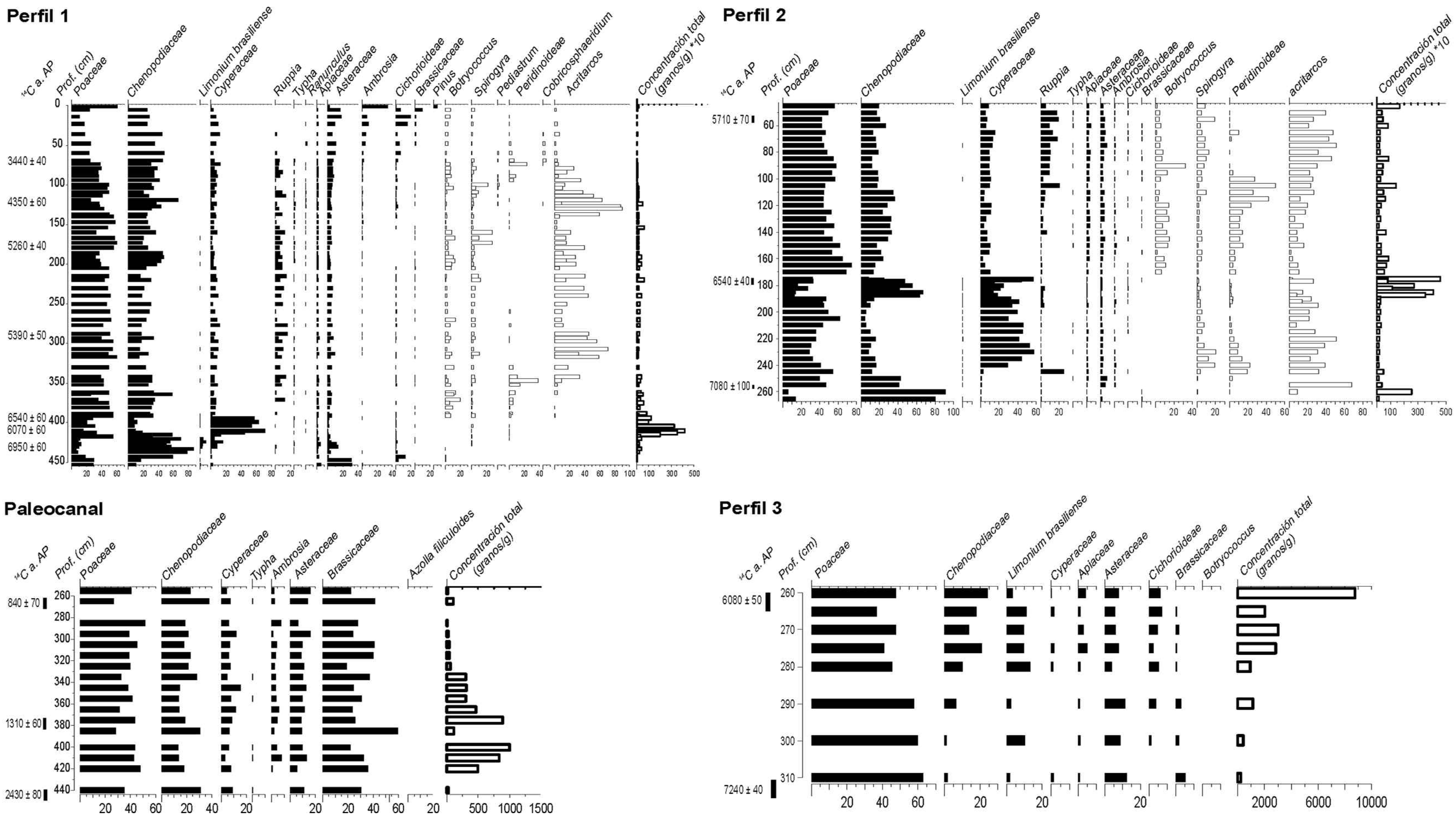

Figura 6. Diagramas palinológicos en porcentajes y concentración polínica total (gramos/gramo) de las cuatro secciones estratigráficas estudiadas en el Arroyo Claromecó (ver Fig. 5) (modificado de Vilanova *et al.*, 2010).

en el supuesto de que los porcentajes polínicos reflejan la vegetación local y regional, utilizando el polen fósil como un registro *proxy* directo de la vegetación del pasado sin considerar los sesgos ocasionados principalmente por los procesos de formación de los depósitos aluviales.

A diferencia de lo que ocurre para el Holoceno, la reconstrucción de la vegetación para el Pleistoceno Tardío de la RP proviene exclusivamente del análisis polínico de sucesiones aluviales. Sin embargo, la mayoría de las secuencias tienen escasos niveles con polen y baja diversidad, probablemente debido a los procesos tafonómicos explicados anteriormente. Registros polínicos completos son raros y están representados solamente por una de las secuencias del Arroyo Tapalqué (Perfil 2, Fig. 4) y otra del Río Sauce Grande (sitio 12, Tab. 1). Estos sugieren que entre *ca*. 16.000 y 12.000 años cal AP en amplias áreas del centro y sudoeste de la actual RP se desarrollaron pastizales psammófilos asociados con elementos arbustivos en el sudoeste (Prieto, 2000). En las otras secuencias, los escasos niveles con polen, algunos datados en 36.130 ± 620 ^{14}C años AP (Prieto *et al*., 2003) y 19. 840 ± 310 ^{14}C años AP (Prieto, 2000) y otros sin datar (*e.g*., Borromei, 1995; Grill, 1995; Gutiérrez *et al*., 2011), están representados principalmente por Brassicaceae, que alcanza proporciones de hasta 80% del registro, acompañada por Poaceae y Asteraceae y/o Chenopodiaceae, en proporciones variables. Cuando el polen de Brassicaceae y Asteraceae aparece en altas proporciones y formando agregados, ha sido interpretado como originado por una rápida depositación local en relación con un ambiente disturbado (Prieto, 1989, 1996; Borromei, 1995; Grill, 1997). El disturbio se relacionó con episodios de inundaciones rápidas y repentinas en depresiones de la llanura de inundación, causados por eventos inusuales de precipitación (Prieto, 2000). La analogía se realizó por comparación con los registros de Brassicaceae en tiempos históricos (Fig. 4), donde este taxón, en altos porcentajes, aparece en asociación con polen de otras especies ruderales y de árboles exóticos, como *Eucalyptus* spp. y *Pinus* spp., correspondientes a plantaciones que se iniciaron a finales del siglo XIX en la RP, indicando un disturbio, en este caso de origen antrópico (*e.g*., Prieto *et al*., 2004; Quattrocchio *et al*., 2008).

En síntesis, los registros polínicos de las sucesiones aluviales del Pleistoceno Tardío muestran numerosos niveles estériles y están escasamente datados, como para realizar una reconstrucción comprensiva de la historia de la vegetación de la RP y hacer buenas correlaciones con otras secuencias de Argentina para ese tiempo.

Los depósitos aluviales del Holoceno muestran en general excelentes registros palinológicos, con buena resolución temporal (Tab. 1; Fig. 6), que han permitido realizar reconstrucciones de la vegetación local y regional y del ambiente.

Con las esperables variaciones locales, las secuencias del Holoceno Temprano muestran que las señales polínicas están marcadas por el incremento de las hidrofitas (principalmente Cyperaceae) en el centro de la RP y la expansión de la vegetación herbácea, mayormente representada por pastizales de gramíneas y una reducción de los taxones arbustivos en el sudoeste (Prieto, 2000). Durante la transición Pleistoceno–Holoceno (12.000–10.000 años cal. AP) se produjo el reemplazo de estepas secas por pastizales húmedos (Fig. 7) y una rápida evolución de ambientes lagunares que no fue sincrónico en la RP. Esta información está suplementada con datos polínicos provenientes de otros tipos de secuencias de la RP (Prieto, 1996, 2000).

Un aspecto destacable es la variabilidad que muestran las secuencias palinológicas continentales del Holoceno Medio y Tardío en contraste con las costeras. Las secuencias continentales, principalmente las ubicadas en el sudoeste de la RP (sitios 12, 13, 14, 15, Tab. 1), presentan fluctuaciones abruptas de los principales tipos polínicos (Poaceae, Asteraceae, Brassicaceae, Chenopodiaceae y Apiaceae) para cada registro, con varios niveles estratigráficos con evidencias de preservación diferencial o totalmente estériles, a excepción de las secuencias Arroyo Sauce Chico (sitio 17, Tab. 1), La Toma (sitio 11, Tab. 1) y Terraza II (sitio 12, Tab.1), estas dos últimas ubicadas en el Río Sauce Grande. Las secuencias ubicadas en el centro de la RP (sitios 3, 5, 6, Tab. 1) registran los cambios locales de la vegetación y las diferencias estarían relacionadas con la geomorfología y el tipo de sucesión sedimentaria analizada (ver caso de estudio).

Las secuencias ubicadas próximas a la costa atlántica muestran una gran continuidad espacial y reflejan procesos similares y homologables. En general, presentan espectros palinológicos con buena preservación, con excepción del sitio 16 (Tab. 1) que tiene numerosos niveles estériles (Quattrocchio *et al.*, 1998) y el sitio 7 (Tab. 1) donde los palinomorfos entre *ca.* 3900 y 3000 ^{14}C años AP tienen mala preservación (Vilanova *et al.*, 2006). Las diferencias espacio-temporales están relacionadas con la ubicación de cada secuencia con respecto a la línea de costa durante el Holoceno Medio y Tardío. Los cambios de nivel del mar influenciaron el desarrollo de las comunidades vegetales locales, y las secuencias palinológicas (sitios 2, 7, 8, 10, Tab. 1) registran la historia de la vegetación y de los ambientes en relación con la evolución geomorfológica de las llanuras costeras.

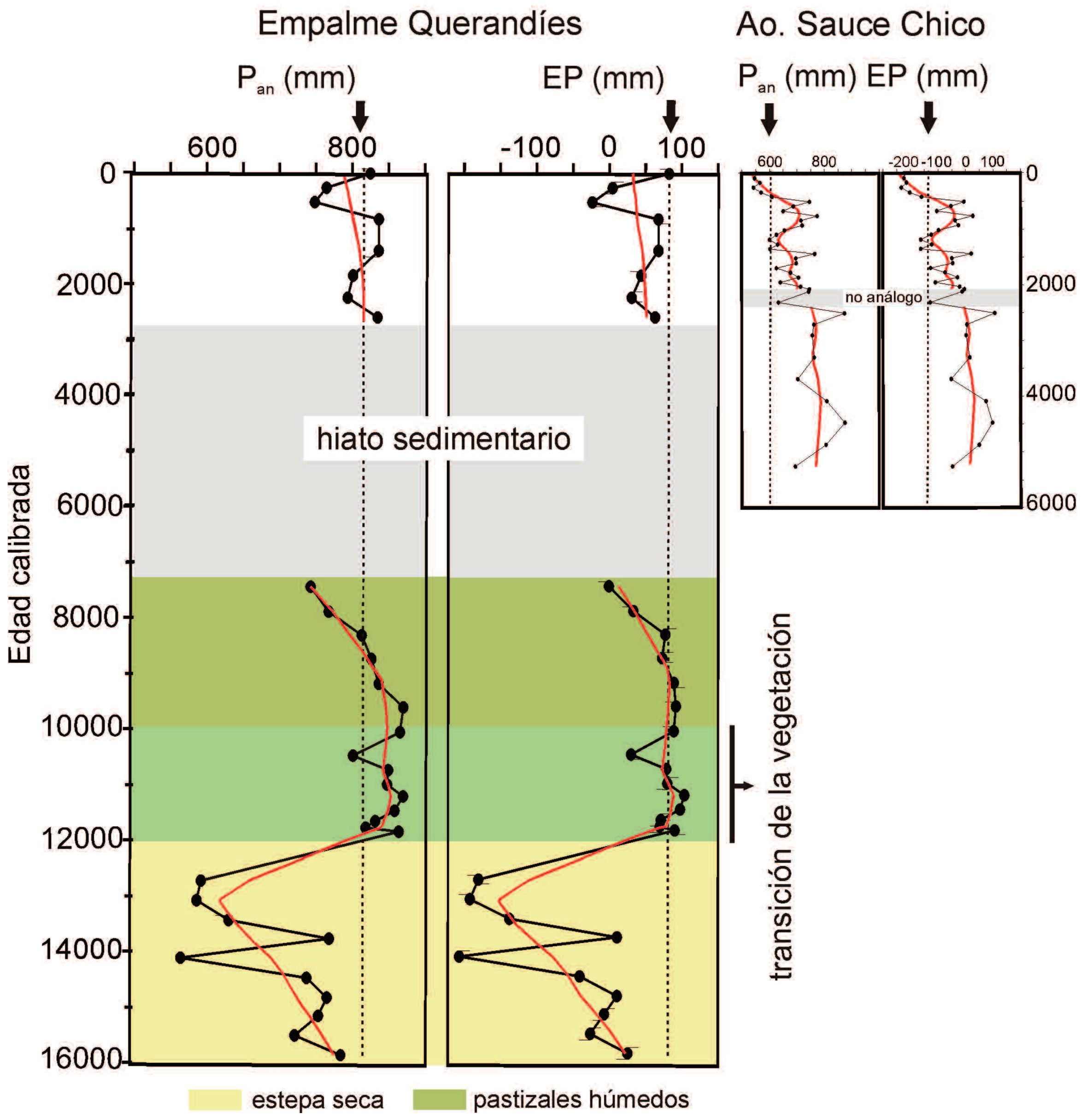

Figura 7. Cronología de las tendencias climáticas y cambios de la vegetación en la región pampeana. Curvas de los valores estimados de la precipitación anual (Pan) y la eficiencia de la precipitación (EP) a partir de las secuencias polínicas Empalme Querandíes (sitio 3, Fig. 1) y Arroyo Sauce Chico (sitio 17, Fig. 1). Las flechas y las líneas de puntos indican los valores actuales (modificado de Tonello y Prieto, 2010).

La reconstrucción de la vegetación para el Holoceno Medio y Tardío realizada a partir del análisis polínico de sucesiones aluviales se ha complementado y ajustado con aquellos datos provenientes de otros tipos de secuencias, como las de lagos someros (*e.g.*, Stutz *et al.*, 2012, 2014) que han permitido reconstruir los principales cambios regionales de la vegetación. Las modificaciones de la vegetación durante el Holoceno Medio y Tardío estuvieron relacionadas con cambios en el nivel de base de los ríos y arroyos, la formación de estuarios en sus desembocaduras como consecuencia de las fluctuaciones del nivel del mar y los cambios de las condiciones climáticas durante ese tiempo.

Los trabajos discutidos han demostrado la importancia de estudiar varias secuencias que representan diferentes posiciones a lo largo de la llanura de inundación, con el fin de entender la dinámica de la vegetación y la evolución del ambiente durante el Holoceno dentro de una misma cuenca. La información regionalmente replicable y consistente derivada de secuencias palinológicas de varias cuencas de drenaje en el sureste de la RP, mostró que el análisis palinológico de los depósitos aluviales ha sido útil para reconstruir cambios paleoambientales en las áreas costeras y que son altamente sensibles a los cambios del clima y del nivel del mar.

Los datos polínicos de sucesiones aluviales de la RP (sitios 3, 13, Fig. 1) también han sido utilizados para la reconstrucción de la vegetación natural potencial de América Latina durante el Holoceno Medio (6000 ± 500 ^{14}C años AP), mediante el método de biomización (Marchant *et al.*, 2009).

Reconstrucción del clima

El polen fósil de las sucesiones aluviales se ha utilizado como registro *proxy* indirecto del clima del pasado. Algunas de las inferencias climáticas para el final del Pleistoceno Tardío (anterior a 9900–10.440 ^{14}C años AP) se han basado en la ausencia de polen en las secuencias aluviales (*e.g.*, Quattrocchio *et al.*, 1998, 2008; Grill *et al.*, 2007; Gutiérrez *et al.*, 2011). Estas inferencias son controvertidas y la confiabilidad de las mismas ha sido cuestionada en la sección preservación polínica y tafonomía.

En numerosos trabajos, las inferencias climáticas para el Holoceno a partir de secuencias polínicas de sucesiones aluviales se realizaron utilizando la relación vegetación-polen-clima de manera cualitativa. Uno de los factores que ha dificultado el conocimiento del clima a partir de los registros palinológicos costeros es la influencia marina, cuyos efectos se solapan con los climáticos especialmente durante el tiempo en el que el nivel del mar fue más alto que el actual. Separar esos efectos no es sencillo, porque la mayor parte de las veces ambos interconectan sus causas y efectos. Por tal razón, la utilización de otros datos *proxies* en conjunto con el análisis palinológico en varias de estas secuencias ha facilitado la realización de inferencias climáticas (*e.g.*, Vilanova y Prieto, 2012; Prieto *et al.*, 2014).

La investigación sobre la relación cuantitativa polen-clima en la RP se inició a principios del siglo XXI. Tonello y Prieto (2010) propusieron la aplicación de la técnica de análogos modernos a datos polínicos fósiles provenientes de dos sucesiones aluviales de la RP para obtener estimaciones cuantitativas de la precipitación y la eficiencia de la precipitación durante los últimos *ca.* 16.000 años cal AP (Fig. 7). Por otra parte, varias secuencias polínicas de sucesiones aluviales de la RP fueron incluidas como registros *proxies* para investigar la evolución temporal de las condiciones climáticas regionales del Holoceno Medio (6000 años cal. AP), combinando reconstrucciones a partir de múltiples indicadores y los modelos paleoclimáticos CMIP5/PMIP3 (*Coupled Model Intercomparison Project fifth phase/Paleoclimate Modeling Intercomparison Project 3*) (Prado *et al.*, 2013; Berman *et al.*, 2016).

CONSIDERACIONES FINALES

La presente revisión ha mostrado que el análisis palinológico de sucesiones aluviales es un recurso importante de información paleoambiental para la RP, pero también ha expuesto que no todas las secuencias palinológicas publicadas son adecuadas para hacer reconstrucciones de la vegetación y del clima.

Se han documentado varios casos de depósitos aluviales con muestras polínicamente estériles o con polen comúnmente mal preservado, inclusive en algunos depósitos del Holoceno Tardío, indicando que un deterioro significativo del polen en estos depósitos puede ocurrir a escalas temporales breves. Aunque en este caso no brindarían información sobre la vegetación, la destrucción diferencial del polen es de interés para interpretar procesos tafonómicos, y por lo tanto debería tenerse en cuenta en los análisis paleoambientales. En este contexto, se recomienda no utilizar el término "presencia" de polen de uno o varios taxones para hacer interpretaciones de la vegetación y en cambio utilizarlo para indicar que algún proceso tafonómico ha alterado el espectro polínico (*cf*. Delcourt *et al*., 1980; Rojo *et al*., 2012), porque la "presencia" estaría sugiriendo que los escasos granos de polen que aparecen serían el resultado de la destrucción diferencial y/o mala preservación.

En algunos de los primeros trabajos publicados de la RP se interpretó la vegetación a partir de zonas polínicas con datos insuficientes (*e.g.*, Grill, 1995; Borromei, 1998). Estas interpretaciones son inconsistentes y por lo tanto se recomienda no definir zonas polínicas cuando la mayoría de las muestras son estériles. Las zonas polínicas, entendidas como entidades temporales con composición polínica relativamente uniforme, se corresponden con las comunidades vegetales que son las unidades básicas de la clasificación en ecología vegetal (Seppä y Bennett, 2003) y es a partir de estas zonas polínicas que se interpreta la vegetación.

Las causas de la alteración de los conjuntos polínicos aluviales, aunque relacionadas principalmente con ciclos de hidratación-desecación, degradación microbiana y posible control de facies, han sido escasamente discutidas en la mayoría de los trabajos. Esto señala la necesidad de realizar estudios sobre la preservación polínica diferencial y la cuantificación del polen transportado por los ríos. Sería relevante poner más atención en el conocimiento de los procesos tafonómicos para mejorar la interpretación de los conjuntos polínicos fósiles de los depósitos aluviales. Documentar las clases de preservación polínica (*e.g.*, Cushing, 1967; Delcourt y Delcourt, 1980) podría constituirse en una herramienta de utilidad al momento de analizar estos registros palinológicos para reconstrucciones ambientales. Por el contrario, existen numerosos depósitos aluviales del Holoceno donde la preservación del polen ha sido excelente y no se han observado distorsiones de los conjuntos polínicos debido al transporte fluvial, indicado por la información consistente y replicable derivada de varias secuencias palinológicas ubicadas en el sudeste de la RP.

Aún quedan amplias áreas con depósitos aluviales con excelentes afloramientos, que son potenciales para el análisis palinológico y permitirán ampliar la información regional sobre la vegetación del pasado. Es necesaria una exhaustiva búsqueda de secciones estratigráficas con probabilidades de obtener secuencias palinológicas bien preservadas, teniendo en cuenta que la experiencia ha demostrado que se pueden obtener en una misma sección estratigráfica secuencias con polen bien preservado y otras estériles. Sin dudas, el conocimiento de la geometría del cuerpo, de la variabilidad facial y de la historia geológica de los depósitos aluviales permitirá seleccionar varios perfiles estratigráficos a lo largo de una sucesión aluvial para los análisis palinológicos que brindarán una información espacio-temporal más adecuada y representativa y así, reconstruir la historia de la vegetación y realizar inferencias paleoambientales confiables.

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VOLUMEN TEMÁTICO

POSTGLACIAL VEGETATION AND CLIMATE CHANGES INFERRED FROM A PEAT POLLEN RECORD IN THE RÍO PIPO VALLEY, SOUTHERN TIERRA DEL FUEGO

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Abstract. The pollen analysis from Cañadón del Toro peat bog (54° 49′ 36″ S; 68° 27′ 36″ W), located in an interior valley of the Fuegian Andes, provides information about vegetation and climate changes during the last 13,500 years. The results indicate the postglacial development of steppe-like vegetation under drier and colder conditions than today, followed by the expansion of *Nothofagus* into the valley after 10,350 cal. yr BP. At this time, the predominance of a forest-steppe ecotone suggests warm conditions and an increase in moisture availability. By about 6,700 cal. yr BP, the closed-canopy *Nothofagus* forest spread under cold and wet conditions. The mire environment also reflects the increasing trend of effective moisture changing from an initial minerotrophic Cyperaceae fen to an ombrotrophic *Sphagnum* bog development.

Key words. Vegetation and climate history. Lateglacial-Holocene. Interior valleys. Tierra del Fuego.

Resumen. CAMBIOS DE LA VEGETACIÓN Y CLIMA POSTGLACIAL INFERIDOS A PARTIR DE UN REGISTRO POLÍNICO DE UNA TURBERA EN EL VALLE DEL RÍO PIPO, SUR DE TIERRA DEL FUEGO. El análisis polínico de la turbera Cañadón del Toro (54° 49′′ 36′′ S; 68° 27′ 36′′ W), ubicada en un valle interior de los Andes Fueguinos, brindó información sobre los cambios de la vegetación y del clima durante los últimos 13.500 años. Los resultados indicaron el desarrollo postglacial de una vegetación de estepa bajo condiciones más secas y frías que las actuales, seguidas por la expansión de *Nothofagus* en el valle con posterioridad a los 10.350 años cal. AP. Durante este período, la predominancia del ecotono bosque-estepa sugiere condiciones más cálidas y un incremento en la disponibilidad de humedad. Alrededor de los 6.700 años cal. AP, el bosque cerrado de *Nothofagus* se expande bajo condiciones frías y húmedas. El ambiente de la turbera también refleja el paulatino incremento de humedad efectiva cambiando desde una turbera minerotrófica de Cyperaceae a una ombrotrófica de *Sphagnum.*

Palabras clave. Historia de la vegetación y el clima. Tardiglacial-Holoceno. Valles interiores. Tierra del Fuego.

THE VEGETATION and climate reconstructions after deglaciation from Isla Grande de Tierra del Fuego have been carried out from several pollen records mainly located at low-elevation sites along the Canal Beagle, southernmost part of the island (Markgraf, 1983, 1991, 1993; Heusser, 1989a,b, 1990, 1995, 1998, 2003; Borromei and Quattrocchio, 2001, 2007; Pendall *et al.*, 2001; Grill *et al.*, 2002; Markgraf and Huber, 2010; Borromei *et al.*, 2014). In contrast, few palynological studies consider the inner valleys of the Fuegian Andes (Borromei, 1995; Mauquoy *et al.*, 2004; Borromei *et al.*, 2007; Borromei and Quattrocchio, 2008), or at high-elevation sites (Markgraf, 1993; Borromei *et al.*, 2010; Markgraf and Huber, 2010). Taken together, the pollen data show a deglacial open ground vegetation dominated by grasses, dwarf shrub heaths and scrubs, with scattered *Nothofagus* Blume 1850 trees. After 11,500 cal. yr BP, the *Nothofagus* woodland containing grasses, composites, and ferns dominated the landscape under warmer and drier climatic conditions than today, and high fire activity. The closed-canopy forest developed after *ca.* 7000 cal. yr BP, under colder and wetter climate conditions. These changes in vegetal paleocommunities have been interpreted in terms of variations in the amount of precipitation of westerly origin related to shifts in the latitudinal location and/or strength of the Southern Westerly Winds (SWW), Antarctic sea-ice extent, and position of the Antarctic Polar Front (Markgraf and Huber, 2010; Kilian and Lamy, 2012).

The mountain valleys of the Fuegian Andes, tributaries to the Canal Beagle valley, show the effect of extensive Pleistocene glacier erosion (Coronato, 1995; Rabassa *et al*., 2000). These valleys were occupied by multiple alpine-type glaciers, ranging from 20 to 30 km in length, though smaller, single-valley glaciers were also present (Rabassa, 2008). They were fed by local cirques, independent of the Cordillera Darwin mountain ice sheet, from where the main glacier (the Beagle Glacier) was nourished. As in all interdependent ice system, the glacial activity in these tributary valleys was controlled by the glaciological behavior of the main ice stream and regional climatic variations. Most likely, these local glaciers were more severely affected by the abrupt climate change, and thus receded fast (Coronato, 1990; Rabassa, 2008).

The present contribution gives insight into the regional and local vegetation dynamics for the interior Andean valleys on the Andean Pacific slope during the last 13,500 yr. The studied peat core was collected from a peat bog (Cañadón del Toro, Fig. 1.1–2) located into the Río Pipo valley, which constitutes the oldest pollen record from low interior valleys. The pollen/spores analysis provides valuable information about the development of plant communities and environmental changes since deglaciation. The results are compared with other pollen records retrieved from sites located at different altitudes in the southernmost part of Tierra del Fuego (Tab. 1) to obtain a better understanding of the regional vegetation and climate patterns during the Lateglacial and Holocene times.

ENVIRONMENTAL SETTING

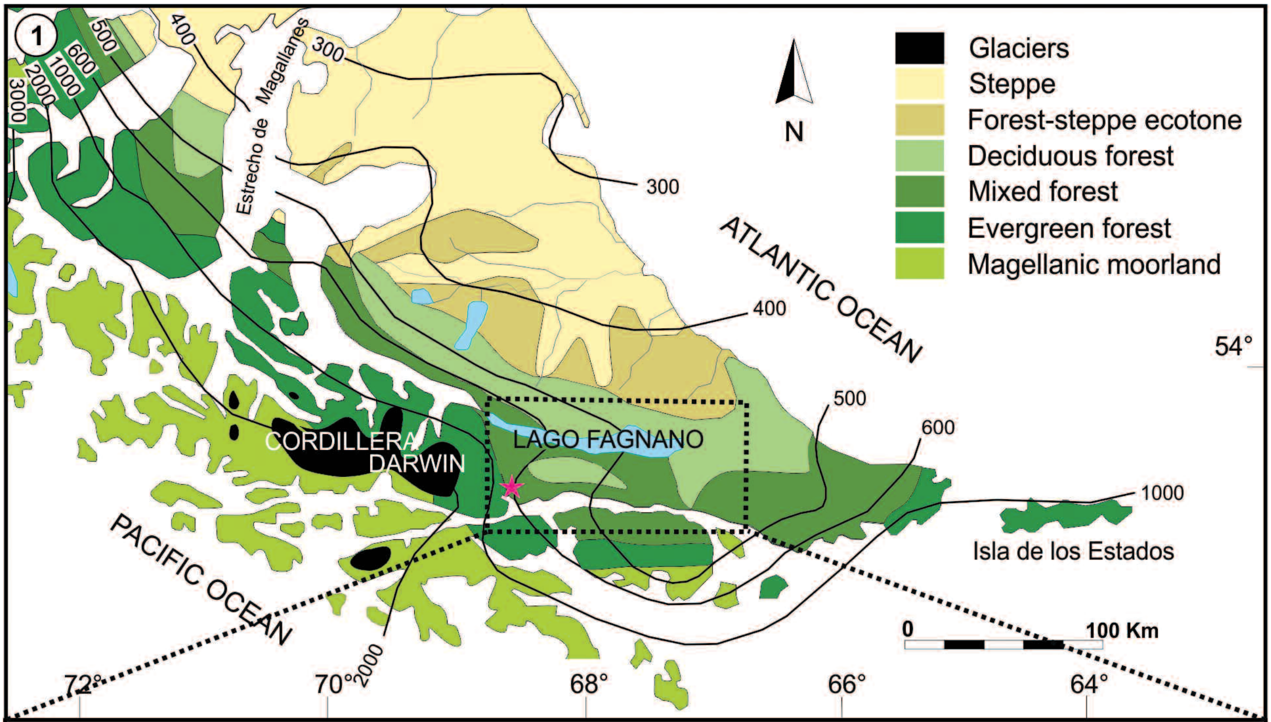
The studied site, herein named as Cañadón del Toro (TCT), is a raised bog (54° 49′ 36′′ S; 68° 27′ 36′′ W; 90 m a.s.l., Fig. 1.3–4) located in the Río Pipo valley, Tierra del Fuego National Park, 3 km north of Canal Beagle coast, in the southern part of Isla Grande de Tierra del Fuego. Canal Beagle is a marine channel 200 km long on a W–E trend and constitutes a connection between the Atlantic and Pacific oceans. It is a former tectonic valley that was completely covered by ice during the Last Glacial Maximum (LGM) (Rabassa *et al*., 2000), with ice limits reaching a maximum extent by *ca*. 25,000 cal. yr BP (Rabassa, 2008).

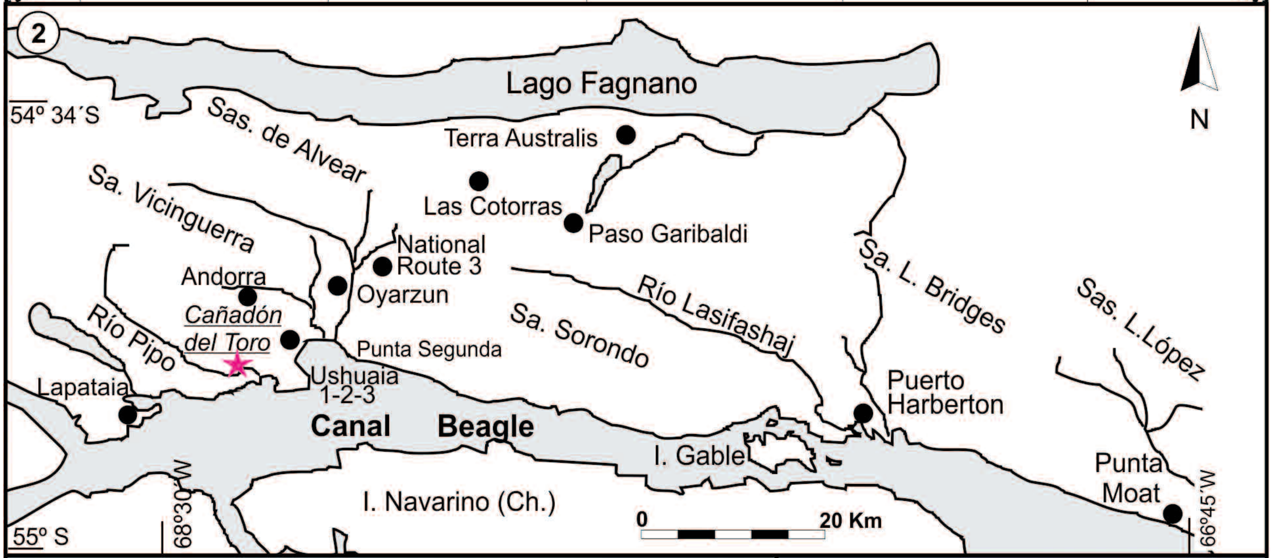
The peat bog reported in this study is 70 ha in extent. It was developed in a glacial basin, and then transformed into a lake, located between the Cañadón del Toro terminal moraines and the sub-glacially eroded rocky hills which enclose part of the valley 2 km to the east. The sides of the lake received colluvium deposits from the valley (Coronato, 1993). The peat bog forms an ombrotrophic type with hummocky surface formed mainly by *Sphagnum magellanicum* Brid. 1798 and *S. fimbriatum* Wilson in J. D. Hooker 1847 and covered by *Empetrum rubrum* Vahl ex Willd. 1806 with minor amounts of Cyperaceae, Juncaginaceae and Juncaceae, and scattered low shrubby *Nothofagus antarctica* (Forster f.) Oersted 1871. It is surrounded by forest communities of *N. pumilio* (Poeppig and Endl.) Krasser 1896.

MODERN CLIMATE AND VEGETATION

The climate of Isla Grande de Tierra del Fuego is determined by its upper middle-latitude location in the belt of prevailing SWW, in the path of eastward moving cyclones, not far from the Antarctic ice. The latitudinal position and strength of the SWW are controlled by the intensity and latitudinal location of the subtropical high-pressure cells in the Pacific and the circum-Antarctic low-pressure trough (Tuhkanen, 1992). Regional climate is highly oceanic in the

Figure 1. 1, Modern-day vegetation map of the Isla Grande de Tierra del Fuego with the mean annual precipitation (mm) isohyets and the peat core location (pink star). The highlighted area in the rectangle is shown enlarged in b (modified from Tuhkanen, 1992). **2,** Location of the study sites as well as of the other sites referred to in the text. **3,** Overall view of Cañadón del Toro peat bog to the northwest; low hills covered by forest are the terminal moraines of the Cañadón del Toro valley. **4,** Detail photograph of the coring site; at the back La Portada rocky-hill which limits the valley to the south.


1
Glaciers
Steppe
Forest-steppe ecotone
Deciduous forest
Mixed forest
Evergreen forest
Magellanic moorland
N
Estrecho de Magallanes
ATLANTIC OCEAN
PACIFIC OCEAN
CORDILLERA DARWIN
LAGO FAGNANO
Isla de los Estados
300
400
500
600
1000
2000
3000
54°
72°
70°
68°
66°
64°
0
100 Km


2
Lago Fagnano
N
54° 34´S
55° S
68°30´W
66°45´W
Sas. de Alvear
Sa. Vicinguerra
Terra Australis
Las Cotorras
Paso Garibaldi
National Route 3
Andorra
Oyarzun
Cañadón del Toro
Río Pipo
Punta Segunda
Ushuaia 1-2-3
Lapataia
Sa. Sorondo
Río Lasifashai
Sa. L. Bridges
Sas. L.López
Puerto Harberton
Canal Beagle
I. Gable
I. Navarino (Ch.)
Punta Moat
0
20 Km


3

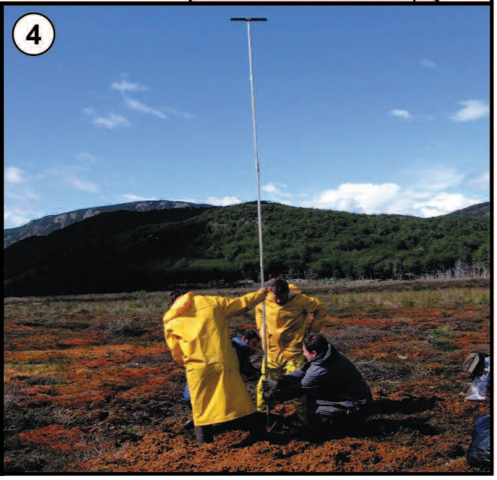

4

TABLE 1 – Late Quaternary pollen records from different peat bogs and exposures of Isla Grande de Tierra del Fuego discussed in this study. The sites are listed according to their altitude above sea level (m a.s.l).

Pacific Andean slope	*Sites*	*Altitude (m.a.s.l.)*	*Lat. South*	*Long. West*	*Core depth (cm)*	*Age range (ka cal BP)*	*References*
Low Andean valleys	*Cañadón del Toro*	*90*	*54° 49′*	*68° 27′*	*678*	*0–13.5*	*This paper*
	Valle de Carbajal	*140*	*54° 44′*	*68° 12′*	*580*	*0–?* *Late Glacial*	*Borromei* et al. *(2007)*
	Valle de Andorra	*180*	*54° 45′*	*68° 18′*	*690*	*0–10.5*	*Borromei (1995)*
	National Route 3	*270*	*54° 43′*	*68° 90′*	*exposure*	*12.0*	*Borromei* et al. *(2007)*
High Andean valleys	*Las Cotorras*	*420*	*54° 41′*	*68° 02′*	*480*	*0–8.0*	*Borromei* et al. *(2010)*
	Paso Garibaldi	*420*	*54° 43′*	*67° 50′*	*306*	*0–14.0*	*Markgraf and Huber (2010)*
Lowlands (Canal Beagle coast)	*Ushuaia 3*	*7*	*54° 48′*	*68° 23′*	*550*	*0–13.9*	*Heusser (1998)*
	Puerto Harberton	*10*	*54° 52′*	*67° 53′*	*104*	*0–17.7*	*Heusser (1990); Markgraf and Huber (2010)*
	Lapataia	*18*	*54° 51′*	*68° 32′*	*510*	*0–11.6*	*Heusser (1998)*
	Punta Moat	*40*	*54° 58′*	*66° 44′*	*450-100*	*5.0–11.2*	*Borromei* et al. *(2014)*
	Ushuaia 2	*80*	*54° 47′*	*68° 18′*	*820*	*0–14.4*	*Heusser (1998)*
	Ushuaia 1	*280*	*54° 47′*	*68° 23′*	*700*	*0–13.8*	*Heusser (1998)*

west and south parts of the archipelago and increasing continental towards the east and north. The daily temperature in summer (January) at Ushuaia averages 9.2° C and in winter (July) 1.6° C; the mean annual precipitation is 574 mm (Prohaska, 1976).

Vegetation composition follows the climatic and topographic gradients across Tierra del Fuego (Moore, 1983; Tuhkanen, 1992) (Fig. 1.1). The modern vegetation in the north corresponds to the Fuego-Patagonian Steppe with a mean annual precipitation less than 400 mm. The tussock grassland of *Festuca gracillima* Hooker f. 1847 covers the area, grading into scrub of shrubby composites or into dwarf shrub heaths of *Empetrum rubrum* (Moore, 1983; Collantes *et al*., 1989). Contact of steppe with deciduous forest occurs through an ecotone under precipitation of 350 to 500 mm annually (Tuhkanen, 1992). Subantarctic Deciduous Forest is represented by two species of southern beech, *Nothofagus pumilio* (lenga) and *N. antarctica* (ñire), which grow to an average altitudinal limit of 550–600 m a.s.l. and become dominant where precipitation exceeds 450 mm yr^{-1}. Towards the south and west of Tierra del Fuego, the annual precipitation rises to over 700 mm and the Subantarctic Evergreen Forest develops, which is dominated by *N. betuloides* (Mirbel) Oersted 1871 (guindo), accompanied by *Drimys winteri* Forster and Forster f. 1775 (canelo), *Maytenus magellanica* (Lam.) Hooker f. 1847 (maitén) and abundant ferns and mosses. Initially, *N. betuloides* is intermingled with *N. pumilio* in an association distinguished as Mixed Evergreen-Deciduous Forest which can be better considered as ecotonal between the two communities (Moore, 1983).

Magellanic moorland occurs beyond the forest along the exposed outermost coast under conditions of increased precipitation (>1500 mm yr^{-1}), high winds and poor drainage. It consists of a mosaic of barren rock, marginal grassland, cushion bogs, scrub, and fragments of evergreen forest (Moore, 1983). Above treeline in the Fuegian cordillera, Andean tundra is comprised of cushion plants, dwarf shrub heaths, and meadow communities (Pisano, 1977; Heusser, 2003).

MATERIAL AND METHODS

Stratigraphy and chronology, age-depth model

A 678 cm sediment-peat core (221 samples) from the mire was obtained using a Russian-type peat corer (chamber length 0.5 m and 5 cm diameter) (Fig. 1.4). During sectioning of the samples, the morpho-stratigraphic consistency was preserved. Thus, the first 50 cm were taken in varying thicknesses by high morphological variability of peat. The remainder of the core was taken every 2 or 3 cm thick. The volcanic ash layer was also individualized. Eleven AMS radiocarbon age determinations established the chronology for the section (Tab. 2). They were obtained at Ångström Laboratory-Tandem Laboratory, Uppsala University (Sweden), and at National Accelerator Centre (CNA, CSIC, Sevilla, Spain). Calibrated dates were calculated using the program CALIB 7.1 software (Stuiver *et al.*, 2015) and the Southern Hemisphere curve SHCal13 (Hogg *et al.*, 2013). The average dates, taking into account the maximum probability interval at 2 sigma ranges, which is considered a robust statistical value (Telford *et al.*, 2004), were used to build an age-depth model by linear interpolation (Fig. 2).

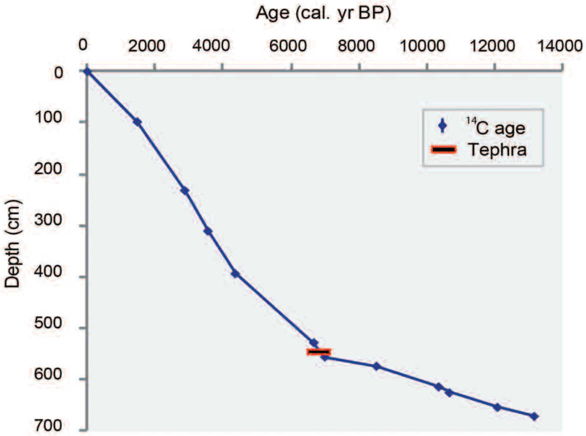


Figure 2. Age-depth model for the Cañadón del Toro peat core.

TABLE 2 – Radiocarbon and calibrated ages from Cañadón del Toro peat core.

Samples	*Depth (cm)*	*^{14}C age (BP)*	*Cal age (BP)*	*Maximum 2σ BP*	*Minimum 2σ BP*	*δ^{13} C ‰*	*Sample material*	*Analysis No.*
TCT-26	*100*	*1655 ± 25*	*1504*	*1564*	*1425*	*-27.1*	*peat*	*Ua-35766*
TCT-69	*233*	*2830 ± 30*	*2887*	*2968*	*2784*	*-26.6*	*peat*	*Ua-35767*
TCT-94	*312*	*3380 ± 35*	*3573*	*3644*	*3464*	*-27.0*	*peat*	*Ua-35768*
TCT-121	*395*	*3980 ± 35*	*4376*	*4516*	*4470*	*-27.2*	*peat*	*Ua-35769*
TCT-164	*529*	*5910 ± 40*	*6689*	*6790*	*6558*	*-27.3*	*peat*	*Ua-35771*
TCT-173	*556*	*6170 ± 70*	*7019*	*7178*	*6796*	*-28.66*	*tephra*	*CNA442*
TCT-179	*575*	*7800 ± 50*	*8531*	*8627*	*8422*	*-27.6*	*peat*	*Ua-35773*
TCT-192	*615*	*9235 ± 55*	*10,359*	*10,507*	*10,237*	*-27.4*	*peat*	*Ua-35774*
TCT-196	*626*	*9490 ± 55*	*10,689*	*10,516*	*10,811*	*-27.4*	*peat*	*Ua-35775*
TCT-210	*654.5*	*10,290 ± 65*	*11,959*	*12,175*	*11,705*	*-27.6*	*peat*	*Ua-35776*
TCT-218	*671.5*	*11,280 ± 120*	*13,098*	*13,320*	*12,800*	*-32.79*	*organic matter*	*CNA443*

All dates mentioned in this paper are given as calibrated years (BP).

Geochemical analysis

Inorganic ash content was obtained by dry ashing at 600 °C for 12 hours (Pontevedra-Pombal *et al.*, 2013), expressing the results as the percentage of dry peat mass (105 °C) according to the equation:

Ash (%)= (a/b) x 100

where a is the weight of the burned sample, and b is the weight of the dried sample at 105 °C.

The content of aluminum extractable with pyrophosphate (Alp) was determined from an extraction with 0.1 M Na-pyrophosphate (pH 10) in a sample/solution ratio of 1:100, which was stirred for 16 hs. The obtained suspension was centrifuged (15 min at 2500 rpm, with three drops of 'superfloc') (Buurman *et al.*, 1996) and the supernatant filtered. Aluminium in the extracts was measured using flame atomic absorption spectrometry. The results, which are the mean of duplicate analysis that are less than 10% apart, are expressed to oven dry weight (105° C).

The X-ray diffraction (XRD) allows identifying the mineral components and the crystalline state of a sample. The amorphous phases generate a broad diffuse pattern, which helps increase the background noise in the form of broad bands. For analysis of the mineral composition of the tephra, 0.05 g of finely ground and homogenized sample was used. The equipment used was a PW1710 Philips Diffractometer with a PW1820/00 vertical goniometer and Bragg-Brentano θ/2θ geometry, generator with glass tube of 2.2 kW, PW 2773/00 Cu anode, PW1711/10 proportional detector, and PW1752/00 graphite monochromator. The measurement time was 1 second per step (step: 0.02°, 2-65° 2Theta). EVA DIFFRAC plus software (Bruker AXS 2001) was used for semi-quantification.

Pollen/spores analysis

The samples were prepared in the Laboratorio de Palinología (INGEOSUR-CONICET, Universidad Nacional del Sur, Argentina) according to standard techniques (Faegri and Iversen, 1989). Prior to treatment, *Lycopodium clavatum* spore tablets (Stockmarr, 1971) were added to each sample in order to calculate pollen concentration per gram of sediment (grains gr^{-1}). Frequencies (%) of tree, shrub and herb pollen were calculated from sums mostly of $\geq$300 grains. Frequencies (%) of pollen of aquatic plants and spores of cryptogams were calculated separately and related to the sum of the total land pollen (TLP). "Other shrubs and herbs" include taxa with low frequency values, such as *Berberis* L. 1753, Brassicaceae, Chenopodiaceae, Asteraceae subf. Cichorioideae, *Astelia pumila* (Forster f.) Gaudich. 1825, *Latua* Phil. 1858, Labiateae, Plumbaginaceae, and *Plantago* L. 1753 We combined pollen from the evergreen species *N. betuloides* and the deciduous *N. pumilio* and *N. antarctica*, given the difficulty in species separation and report these as "*Nothofagus dombeyi*-type".

Plotting of palynological diagrams and statistical analysis were carried out using Tilia 2.0.1 program (Grimm, 2004). The pollen/spores spectrum was subdivided into zones based on visual inspection of the pollen record and a stratigraphically constrained cluster analysis using Edwards and Cavalli-Sforza's chord distance (TGView 2.0.2, Grimm, 2004). For the analysis, all taxa with percentages of $\geq$1% of the sum of terrestrial pollen were included. The fossil pollen spectra were compared with modern pollen datasets from surface soil samples (Heusser, 1989a; Trivi de Mandri *et al.*, 2006; Musotto *et al.*, 2012) and with present-day plant formations from Tierra del Fuego (Pisano, 1977; Heusser, 2003).

RESULTS

Stratigraphy and chronology

The studied core consisted of organic rich layers interspersed with bluish gray clays [678–624 cm]. The overlying sediments consisted of strongly decomposed black peat [624–584 cm], changing into moderately decomposed dark brown peat [584–557 cm]. A 13-cm-thick tephra layer [557–544 cm] was recognized. From 544 to 520 cm the core consisted of highly humified brownish black peat, which was overlain by dark brown peat between 520 and 403 cm. From 403 to 74 cm the core consisted of dark brown *Sphagnum* peat interspersed with reddish *Sphagnum* peat containing woody detritus. The upper 74 cm of the core were composed by reddish unhumified *Sphagnum* peat.

In the range of *ca.* 570–534 cm a turnaround in the inorganic material concentration (ash) is detected. At an average depth of 550 cm, this drastic increase represents a rise of almost 6 and 12 times the ash content detected in the first (from *ca.* 10,100 to 8500 cal. yr BP; average: 7.02%) and second (last 6800 cal. yr BP; average: 2.55%) ombrotrophization cycles, respectively (Fig. 3). This inorganic material has a high content of Alp indicating their high reactivity, characteristic of amorphous organomineral complex (Garcia-Rodeja *et al.*, 2004). In correlation with this chemical feature, the X-ray diagram is clearly dominated by a large amorphous band (noise) where amorphous quartz and albite are detected, typical of an andesitic volcanic ash (Fig. 4).

The tephra layer was dated at 6170 +/- 70 ^{14}C yr BP (556–553 cm; 7178–6796 cal. yr BP). The source of this tephra is unknown, but its age is similar within statistics to the age of the greenish andesitic tephra derived from a large explosive eruption (H_1) of the Volcán Hudson (45° 54′ S; 72° 58′ W, 1905 m a.s.l.), regionally dated 7960–7423 cal. yr BP (Stern, 2008), and widely distributed in Tierra del Fuego. This volcano is located in the southern portion of the Zona Volcánica Sur (ZVS, 33°-46° S), more than 900 km farther northwest. H_1 has also been identified in the Harberton raised bog (Kilian *et al.*, 2003), 75 km east of TCT. X-ray spectra obtained for the tephra located in TCT and Harberton raised bog show a close resemblance (Fig. 4).

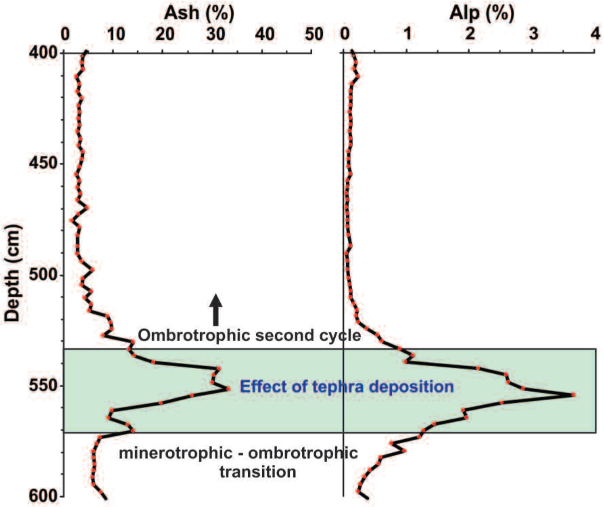


Figure 3. Effect of deposition of tephra on the inorganic ash and sodium pyrophosphate extractable Al content in Cañadón del Toro peat bog.

Pollen/spores analysis

The pollen record from Cañadón del Toro has been divided into three local pollen assemblage zones, CDT-1 to CDT-3 (Fig. 5). Zone CDT-3 was divided into three subzones. The main pollen concentration values (Fig. 6) were calculated in order to assess the independent behavior of pollen types and to add a new dimension to the study of vegetation history. From the lower to the upper part of the section, they are:

Zone CDT-1 (678–613.5 cm; 13,500–10,350 cal. yr BP). This zone is characterized by the dominance of Poaceae (28–77%), accompanied by Asteraceae subf. Asteroideae (48%), *Acaena* Mutis ex L. 1771 (32%), *Empetrum rubrum* (28%), *Gunnera* L. 1767 (12%), and *Caltha* L. 1753 (<10%). Other herbaceous taxa such as Rubiaceae, Apiaceae, *Gentiana* L. 1753, Caryophyllaceae and *Azorella* Lam. 1783 are present with low frequencies (<5%). *Nothofagus dombeyi*-type records low values (0.3–13%) increasing towards the end of the zone (23%). Cyperaceae shows percentages of 43% at the base and increases rapidly to reach its maximum abundance (68%) followed by an abrupt decline toward the end of the zone (3%). Total pollen concentration is low (3000 grains gr^{-1}) at the onset of the sequence increasing up to 191000 grains gr^{-1} towards the end of the zone. It is contributed mainly by Poaceae (1300–105200 grains gr^{-1}), Asteraceae subf. Asteroideae (165–62500 grains gr^{-1}), and *E. rubrum* (335–4500 grains gr^{-1}). Among the aquatic taxa, Cyperaceae records its highest values up to 171200

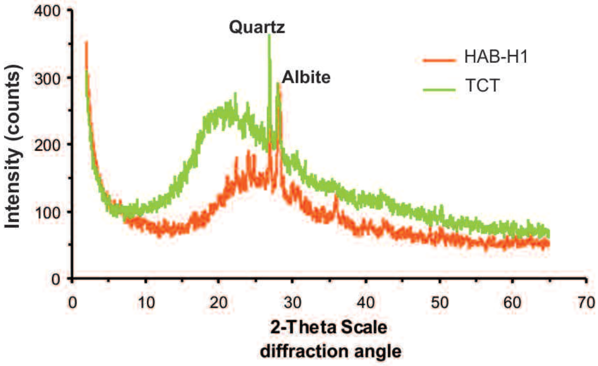


Figure 4. X-ray spectra of Haberton (**HAB-H$_1$**) and Cañadón del Toro (**TCT**) peat bogs.

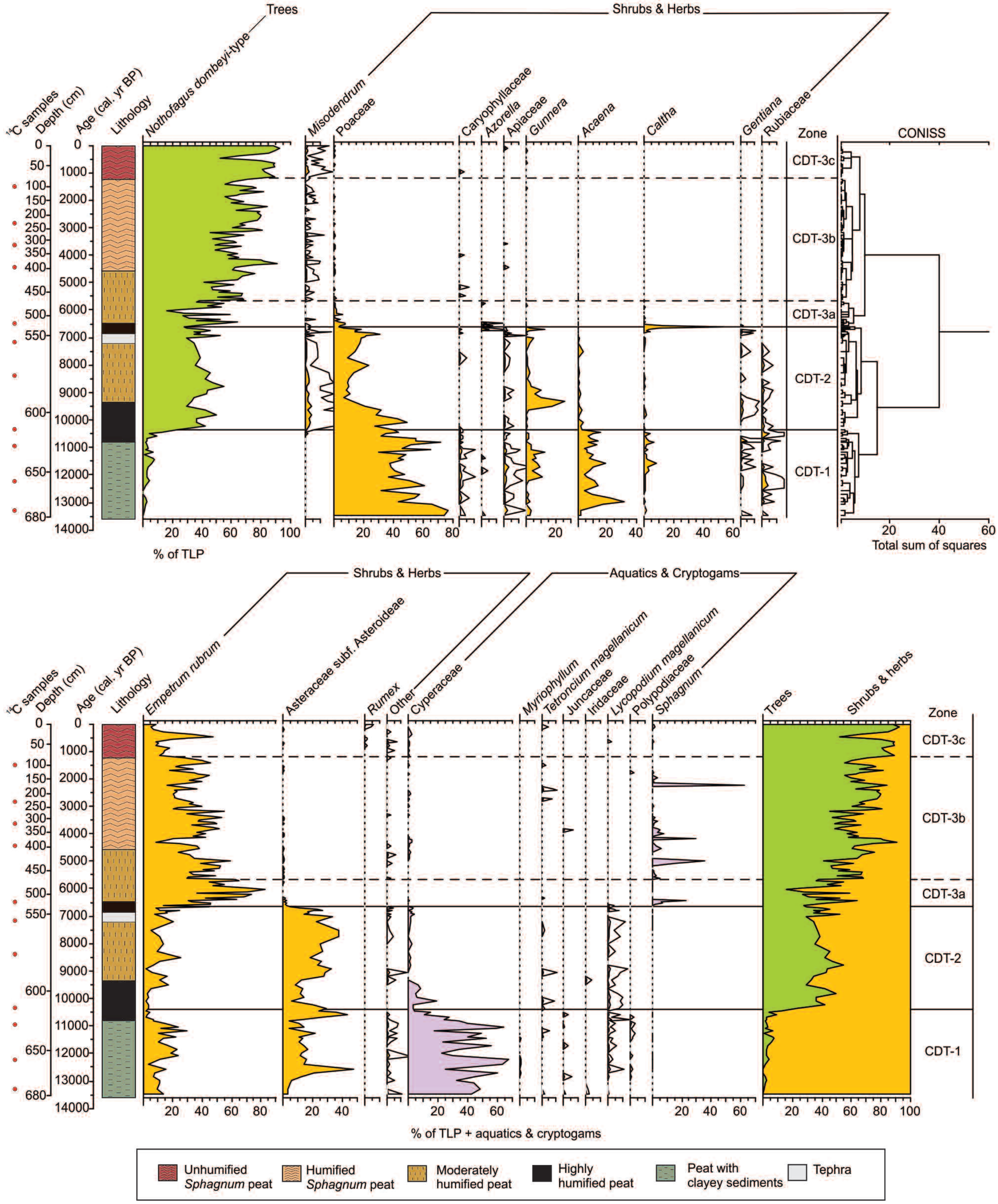


Figure 5. Fossil pollen/spore frequency (%) diagram and lithology at Cañadón del Toro mire. Outline curve represents an exaggeration percentage curve (10x) for minor taxa.

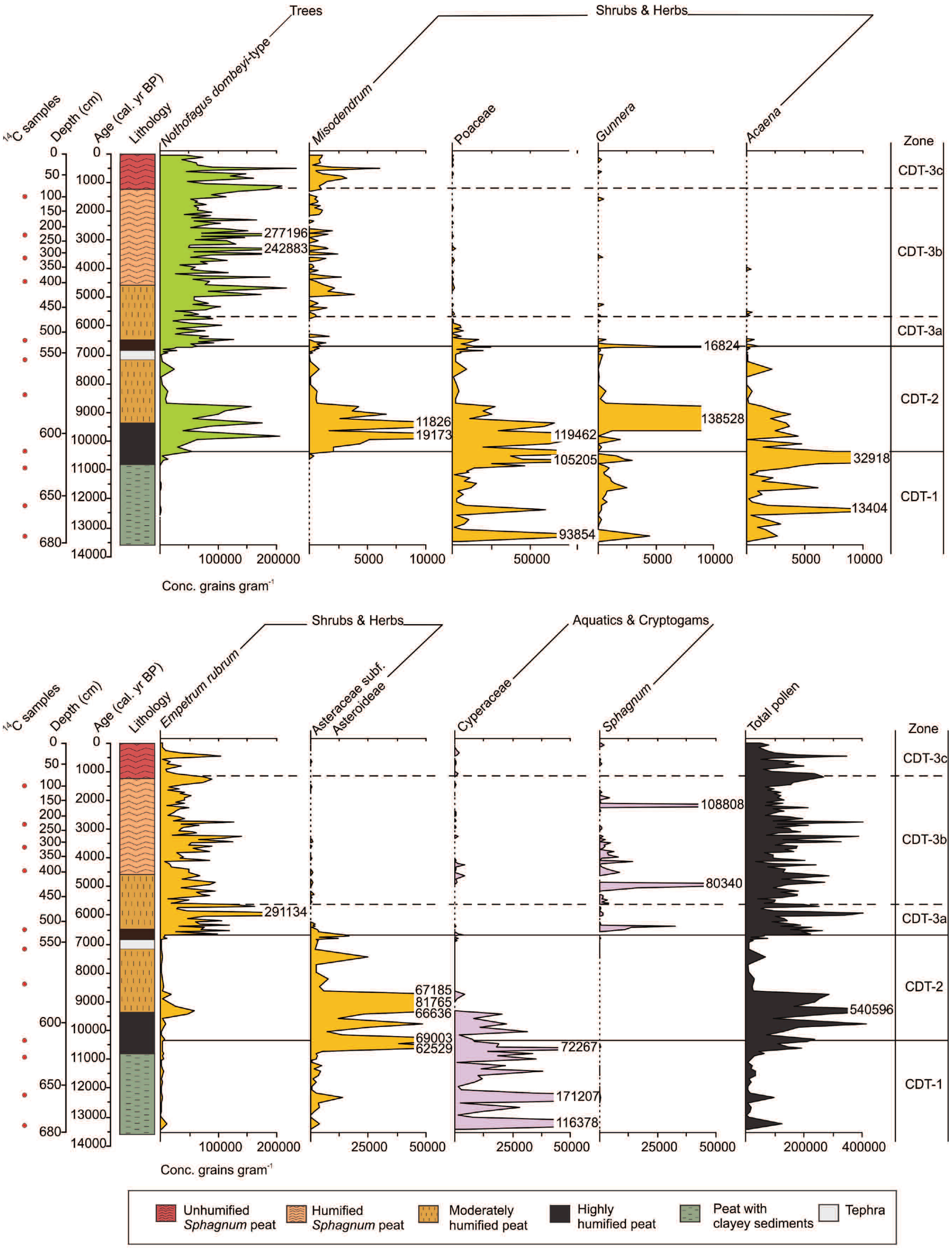


Figure 6. Fossil pollen concentration diagram (grains gram^{-1}) and lithology at Cañadón del Toro peat bog.

grains gr^{-1}. *N. dombeyi*-type concentration is less than 5500 grains gr^{-1} throughout the zone.

Zone CDT-2 (613.5–530.5 cm; 10,350–6700 cal. yr BP). In this zone *Nothofagus dombeyi*-type (29–55%) expands abruptly along with decreases in Poaceae (8–49%), *Acaena* (<4%) and *Caltha* (<4%). Asteraceae subf. Asteroideae (38%) and *Empetrum rubrum* (25%) maintain similar percentages compared with those of the previous zone CDT-1. *Misodendrum* Banks ex DC. 1830, a hemiparasite on *Nothofagus* species, appears in low values (5%). *Gunnera* (26%) reaches its highest abundance in the record followed by its decline toward the end of the zone. Among the aquatic taxa, Cyperaceae decreases to <19%. Total pollen concentration exhibits an increasing trend (up to 540–600 grains gr^{-1}) in the lowermost part of the zone. *N. dombeyi*-type (206500 grains gr^{-1}), Poaceae (119500 grains gr^{-1}), Asteraceae subf. Asteroideae (81800 grains gr^{-1}) and *E. rubrum* (57500 grains gr^{-1}) show high values, while Cyperaceae declines (22000 grains gr^{-1}). Total pollen concentration values record an abrupt decline (<66500 grains gr^{-1}) between 8800 and 7000 cal. yr BP, increasing toward the end of the zone up to 73400 grains gr^{-1}.

Zone CDT-3 (530.5–0 cm; 6700–0 cal. yr BP). Three subzones can be differentiated on the basis of proportional changes between *Nothofagus dombeyi*-type and *Empetrum rubrum*.

Subzone CDT-3a (530.5–469.5 cm; 6700–5650 cal. yr BP). This subzone displays an increase in *E. rubrum* (14–82%). *N. dombeyi*-type (16–59%) maintains similar frequencies compared with those of the previous zone CDT-2. *Caltha* peaks at 53% at the beginning of the subzone followed by its virtual disappearance. Poaceae (7%) displays low values. *Sphagnum* records 23%.

Subzone CDT-3b (469.5–81.5 cm; 5650–1200 cal. yr BP). During this subzone *N. dombeyi*-type shows an increase in its percentages (41–81%) along with decreases in *E. rubrum* (8–58%). *Sphagnum* reaches three peaks, up to 30, 36 and 62%.

Subzone CDT-3c (81.5–0 cm; 1200–0 cal. yr BP). This subzone is characterized by an increase in *N. dombeyi*-type (up to 93%), while *E. rubrum* (18%) decreases in relation to the previous Subzone CDT-3b. Between 510 and 380 cal. yr BP, *N. dombeyi*-type registers low frequency values (52–67%), while *E. rubrum* increases up to 47%.

In this zone total pollen concentration records its highest values (405800 grains gr^{-1}). The main contributor is *N. dombeyi*-type that reaches up to 277200 grains gr^{-1}. *E. rubrum* records 140200 grains gr^{-1} with a peak of 291100 grains gr^{-1}.

DISCUSSION

Local glacial history

In the Canal Beagle area, the LGM (*ca.* 25,000 cal. yr BP; Rabassa, 2008) is represented by a complex system of basal, lateral and terminal moraines. The latter moraine is located at Punta Moat, 120 km to the east of the Río Pipo valley, where Cañadón del Toro peat bog was formed. This event has been locally named Moat Glaciation (Rabassa *et al.*, 1990). Recessional moraines have been identified 100 km west of the frontal position, at Punta Segunda, situated in the north coast of the channel. Although no absolute ages could be obtained from these moraines, a Lateglacial age was inferred (Rabassa *et al.*, 2000).

Hall *et al.* (2013), based on the basal peat bog date from several sites of Cordillera Darwin (54–55° S; 69–70° W), postulated that a collapse of a massive ice in the cordillera began at 18,400 cal. yr BP, which had progressed such that ice was confined into the interior fjords by 16,800 cal. yr BP. The authors showed evidences that central Canal Beagle must have been free of ice at least at 14,800 cal. yr BP. A basal radiocarbon date from Ushuaia 2 peat bog located in the low terrains (25 m a.s.l.) along the Canal Beagle coast at Ushuaia city, confirms that this area was free of ice by 14,470 cal. yr BP; and by about 13,900 cal. yr BP (Ushuaia 1 peat bog) at elevations of 300 m above Ushuaia city. Eight km to the southwest, the landscape was free of ice by 11,640 cal. yr BP when Lapataia peat bog started to develop (Heusser, 1998).

No Lateglacial re-advances have been located and dated in the lowlands of the Canal Beagle (Rabassa *et al.*, 2006). However, geomorphological evidences from the tributary valleys of Fuegian Andes allowed to identify moraines that demarcated advances of glaciers during the Antarctic Cold Reversal (ACR, 14,500–12,900 cal. yr BP), the Younger Dryas Chronozone (YD, 12,900–11,700 cal. yr BP), and the presence of one, and locally two, closely spaced moraines located up to 2 km downvalley of Little Ice Age (LIA, <1000 cal. yr BP) (Menounos *et al.*, 2013). In these tributary valleys, several moraine deposits related to a Holocene glacier expansion have been identified (Rabassa *et al.*, 1990; Strelin *et al.*, 2001; Planas *et al.*, 2002; Menounos *et al.*, 2013, Ponce *et al.*, 2015). Menounos *et al.* (2013) have reported geological evidences for one or more advances of glaciers sometime between 7960–7340 and 5290–5050 cal. yr BP to limits only tens of meters beyond LIA maximum positions. No absolute ages are yet available for the inner moraines. However, these moraines have been assigned to advances of the LIA (<1000 cal. yr BP) based on their fresh, uneroded forms, proximity to existing ice, and similarity of their positions to moraines in the vicinity that had already been assigned to the LIA (Menounos *et al.*, 2013). These terminal moraines descend to 680±131 m a.s.l. (Ponce *et al.*, 2015). Menounos *et al*. (2013) suggested that the LIA event was the more extended neoglacial advance in the region.

Palaeoenvironmental reconstruction at Cañadón del Toro peat bog

After 13,500 cal. yr BP, the initial Lateglacial vegetal communities that colonized the deglaciated terrain were characterized by the dominance of pioneer grasses (Poaceae) and dwarf shrub heaths (*Empetrum rubrum*). By about 13,000 cal. yr BP, the spread of shrubs (Asteraceae subf. Asteroideae) along with *Acaena*, an indicator of open/disturbed grounds, suggests the prevalence of grassland-shrub environments. With soil development and increased humidity, the landscape was invaded by wetland herbs such as *Caltha*, *Gunnera*, and *Gentiana*. Among the more frequent steppe-associated plants, Apiaceae, Rubiaceae, Caryophyllaceae and *Azorella* were recorded. During this interval, the *Nothofagus* populations were poorly represented with low frequency and concentration values. Meanwhile, mire plants were characterized mainly by the dominance of sedges (Cyperaceae) showing at this initial stage the development of a minerotrophic mire (fen). These vegetal palaeocommunities resemble the present Fuegian steppe of the northern part of Tierra del Fuego, where mean annual precipitation is less than 400 mm and mean annual temperatures average 5.5 °C (Tuhkanen, 1992).

A significant vegetation change occurred by 10,350 cal. yr BP. The steppe environments were replaced by a forest-steppe ecotone that prevailed until 6500 cal. yr BP. During this interval, stands of *Nothofagus* forest were interspersed with shrubs (Asteraceae subf. Asteroideae), grasses (Poaceae), and herbs (*Gunnera*, *Acaena*, Apiaceae, Rubiaceae, and *Gentiana*). The increase in the arboreal frequencies and concentrations together with the persistence in the record of the mistletoe *Misodendrum* seems to be a good evidence for the local presence of *Nothofagus*. Analogous communities exist today in central Isla Grande de Tierra del Fuego, with annual precipitation estimated at 350–500 mm and summer temperatures averaging 11 °C (Tuhkanen, 1992). During this period, the mire environment suggests a transitional stage between Cyperaceae fen and *Sphagnum* bog, due to an increase in atmospheric humidity. Between *ca.* 8600 and 7000 cal. yr BP, the total pollen concentration values drop abruptly, displaying synchronous fluctuations of taxa in the same direction (Fig. 5). Many complex factors such as mechanical, chemical, and biological agents, determine the differential preservation of the pollen in a specific type of deposit (Bryant, 1978). The increase in the ash during this interval (570–534 cm depth, Fig. 3) could reflect the tephra deposition process itself combined with increased mineralization of organic matter derived from the enhancement of microbial activity, resulting in a temporary alteration of trophic and water environment. The low concentration rates may also give some indication of oxidizing conditions at the mire surface probably caused by a seasonally fluctuating water table, which would account for a lack of pollen preservation (Heusser, 1998; Cook, 2009). This is in line with a reduced precipitation pattern and warmer conditions that prevailed during this period. Almost immediately after the tephra deposition, the development of new suitable habitats for pioneer plants is manifested by the increase in *Caltha* and *Gunnera* pollen.

After 6500 cal. yr BP, the pollen assemblage reflects the development of a closed-canopy *Nothofagus* forest spreading into the valley as a response of cooler and wetter conditions. This climate change is also evidenced in the mire setting. The increasing percentages of *Sphagnum* and *E. rubrum* suggest that the mire switched to ombrotrophic conditions. *Sphagnum* species colonize bog surface, whereas

E. rubrum grows on dry, elevated areas such as unhumified hummocks (Birks and Birks, 1980; Markgraf and Huber, 2010). Presently, these vegetal communities develop in the south of Tierra del Fuego with annual precipitation of more than 500 mm (Tuhkanen, 1992). By about 500 cal. yr BP, *Nothofagus* frequencies decline along with an increase in *E. rubrum* pollen, followed by the return of a closed-canopy forest at the site. *Rumex acetosella* L. 1753, an introduced taxon, indicates vegetation disturbance, including logging, fire and grazing (Mancini, 2009).

Comparison with other sites

Lateglacial pollen evidences show a vegetation pattern dominated by a mosaic of highly diverse steppe-like communities with scarce *Nothofagus* trees, at Puerto Harberton, and Ushuaia 2 and 3 sites, situated in the lowlands along the Canal Beagle coast (Heusser, 1990, 1998; Markgraf and Huber, 2010). In the low interior valleys, the pollen records from Cañadón del Toro (this paper), Valle de Carbajal (Oyarzun peat bog), and National Route 3 exposure (Borromei *et al.*, 2007), as well as Paso Garibaldi, a high-elevation site (Markgraf and Huber, 2010), display a broadly similar vegetational pattern. The vegetation probably changed following its own internal dynamics, including the spread of plants and colonization of new ground, competition for suitable habitats and succession (Fontana and Bennett, 2012). During this time, at Puerto Harberton (Fig. 7), the *Nothofagus* pollen data suggest the survival of small tree populations in glacial refugia, distributed within the modern forested areas outside the glacier limits (Premoli *et al.*, 2010; Fontana and Bennett, 2012). It is likely that the early presence of the prostrate shrub *Empetrum rubrum* in the deglaciated valleys may have favoured the regional establishment of *Nothofagus* species (Fontana and Bennett, 2012). Today, the canopy of *E. rubrum* has an important nurse effect on growth of *N. antarctica* seedlings in the early stages of post-glacial succession by influencing microclimate and/or soil resource availability (Henríquez and Lusk, 2005). In Terra Australis mire, at central Tierra del Fuego (Fig. 1), the record of fungal remains of cf. *Microthyrium fagi* Ellis 1977 concurrent with increases in *Nothofagus* frequencies may indicate that some trees were locally present during the Lateglacial period (Musotto *et al.*, 2016). *Microthyrium fagi* is found on dead autumn leaves of *N. pumilio* (Arambarri and Gamundi, 1984); while other microthyriaceous fungi, including cf. *M. fagi*, have been reported in the surface samples from deciduous beech forest (Musotto *et al.*, 2012).

Particularly, in the Cañadón del Toro sequence, there is no indication in the arboreal composition (both frequencies and concentrations) of a major cold reversal related to the ACR and the YD Chronozone. However, Heusser (1998) identified two episodes of cooling characterized by low *Nothofagus* influx and separated by intervals of high arboreal influx associated to warmth conditions, from dated peat bog sections (Puerto Harberton, Ushuaia 1, 2 and 3) located along the Canal Beagle coast.

The expansion of *Nothofagus* woodland (Fig. 7) started during the Early Holocene, by about 11,500 cal. yr BP in the low terrains at Puerto Harberton, eastward Canal Beagle, and earlier, by about 12,400 cal. yr BP, at elevations of 300 m above Ushuaia city (Ushuaia 1 site). In Cañadón del Toro, the development of woodland-dominated vegetation occurred after *ca*. 10,500 cal. yr BP, like in the lowlands at Ushuaia 2 and 3. In the inner valleys of Andorra and Carbajal (Oyarzun site), *Nothofagus* woodland spread later. It seems probable that the expansion of *Nothofagus* has been distinctly affected by the prevailing westerly circulation and the local conditions at different sites (*e.g.*, soil-types, drainage, slope, facing).

During this period, the *Nothofagus* populations along with the steppe communities constituted an ecotone indicating warmer and drier conditions than today. Noticeable is the increase in *Misodendrum* frequencies in all the pollen sequences. This mistletoe is a hemiparasite that thrives exclusively on *Nothofagus* species; the intensity of infestation is dependent upon light and host availability, being maximal under high luminosity conditions and intermediate *Nothofagus* densities (Moreno *et al.*, 2014). High fire frequencies in Tierra del Fuego during the early Holocene must have favoured the development of open ground tracts and, at the same time, retarded the spread of the *Nothofagus* woodland (Whitlock *et al.*, 2007; Markgraf and Huber, 2010). In the Terra Australis record, the mycorrhizal *Glomus* Tul. and C. Tul. 1845 was probably associated with the presence of grasses and shrubs indicating relatively dry environmental conditions, while the fungal spores of *Gelasinospora* Daw. 1933 have been related to fire events in the area during this time (Musotto *et al.*, 2016).

Towards the eastern sector of the Canal Beagle, at Punta Moat site, distant <1 km from the coast-line, the influence of the relative rise of the sea-level and the marine spray-humidity favoured the early development of a closed-canopy *Nothofagus* forest by 9500 cal. yr BP (Borromei *et al.*, 2014) (Fig. 7). Also, in the high-elevation sites, such as Paso Garibaldi and Las Cotorras, the closed-canopy *Nothofagus* forest reached those altitudes by about 8800 and 8000 cal. yr BP, respectively (Fig. 7). Although no charcoal analysis was performed on Las Cotorras peat core, Markgraf and Huber (2010) indicated that fires were absent at the upper treeline at Paso Garibaldi and did not influence the *Nothofagus* communities there. At these elevation sites, the development of a closed-canopy forest suggests modern moisture levels with a treeline at or even above present (Markgraf and Huber, 2010). Meanwhile, dense forest populations developed after about 7000 cal. yr BP in the lowlands along Canal Beagle coast and after 6500 cal. yr BP in the interior valleys (Fig. 7).

There are no clear evidences for the Holocene glacier fluctuations in the vegetation composition of these fossil localities. However, the intervals of low *Nothofagus* influx, at 6380–5000 cal. yr BP, 2334–360 cal. yr BP and recently at Puerto Harberton, are indicative of cooler episodes (Heusser, 1989b). The first interval of decline in arboreal influx at Puerto Harberton may be related to the one of the glacier advances reported by Menounos *et al.* (2013) between 7960–7340 and 5290–5050 cal. yr BP. During the last 1000 years (Fig. 7), decreases in the frequency of *Nothofagus* pollen have been recorded in the Cañadón del Toro valley at *ca.* 500 cal. yr BP. In Las Cotorras, a major vegetational change towards colder conditions has been re-

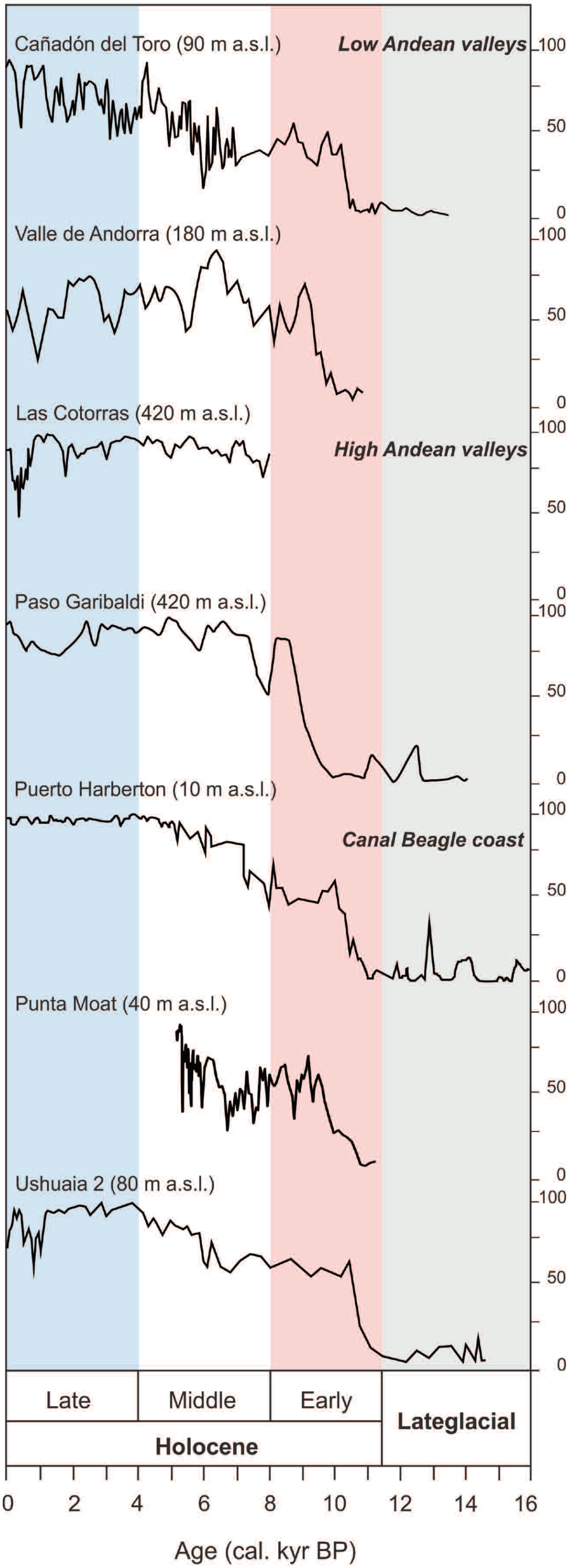


Figure 7. *Nothofagus* pollen frequency records from Cañadón del Toro (this paper); Valle de Andorra (Borromei, 1995); Las Cotorras (Borromei *et al.*, 2010); Paso Garibaldi (Markgraf and Huber, 2010); Puerto Harberton (Markgraf and Huber, 2010); Punta Moat (Borromei *et al.*, 2014); and Ushuaia 2 (Heusser, 1998) sites. The peat bogs are listed according to their altitude above sea level (m a.s.l.).

ported after 1000 cal. yr BP, when the decline of *Nothofagus* pollen reached a minimum between *ca*. 680 and 300 cal. yr BP. During this interval, the stratigraphy of the mire showed peat interspersed with clastic sediments. They were indicative of a clastic input coming from mass wasting events or floods occurring during snowmelt and deposited over a very short time scale (Borromei *et al*., 2010). Presumably, the reduced vegetal cover, due to a less dense forest, favoured the landslides downslope in the valley. The multiproxy analyses of a *ca*. 1400-yr peat record from Valle de Andorra also registered climatic fluctuations including a period of cooler and/or wetter conditions (Mauquoy *et al*., 2004). In Paso Garibaldi high-elevation site, the spread of Andean grasslands along with a less dense forest indicated the treeline lowering below the site between 2500 and 400 cal. yr BP, probably related to minor temperature depressions (Markgraf and Huber, 2010). Taken together, these pollen data could be related to the LIA (<1000 cal. yr BP) chronozone. Climatic factors, such as strength and latitudinal position of the SWW, changes in solar irradiance and in atmospheric-ocean circulation have been mentioned among the more important external drivers for Holocene glacier fluctuations in Tierra del Fuego (Menounos *et al*., 2013).

CONCLUSIONS

The palaeovegetation reconstruction from Cañadón del Toro peat bog show changes in the plant communities that follow similar patterns to those recorded in the lowlands and in the high-elevation sites of the forested region in southern Tierra del Fuego, although these changes were not simultaneous. For most of the Lateglacial period, after *ca*. 13,500 cal. yr BP, the Río Pipo valley remained with scattered *Nothofagus* trees and grasses, shrubs and heaths dominated the vegetation. Initially, the mire was a Cyperaceae fen. *Nothofagus* spread into the valley during the Early Holocene, around 10,350 cal. yr BP, like an ecotone when the climate conditions were warmer and drier than today. The regional fires may have restrained the *Nothofagus* forest expansion favouring the development of open ground vegetation dominated by shrubs and grasses. Meanwhile, the mire showed a transitional physiognomy between Cyperaceae fen and *Sphagnum* bog.

The dated tephra at 6170 +/- 70 ^{14}C yr BP (7178–6796 cal. yr BP) seems to correspond, in chronology and composition, to the H_1 tephra from the Volcán Hudson. The pollen and geochemical spectra of this event record a temporary impact during the development of the peat bog between *ca.* 8600 and 7000 cal. yr BP.

During the mid- to Late Holocene, by about 6700 cal. yr BP, a climatic change towards colder and wetter conditions may have facilitated the expansion of dense forest on the Pacific Andean slope in southernmost Tierra del Fuego. By this time, the mire also changed to ombrotrophic conditions, contributed essentially by *Sphagnum*, reflecting greater water depth and less mineral input. During the last 1000 cal. yr BP, the record showed a decline in the *Nothofagus* frequencies at *ca.* 500 cal. yr BP most probably related to colder conditions. The palaeoenvironmental conditions recorded throughout the studied sequence are closely related to oscillations in precipitation and temperature as a response to the variations in the position and/or strength of the southern margin of the SWW at these high latitudes.

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REVIEW OF THE PALAEOENVIRONMENTAL RECONSTRUCTION OF LATE QUATERNARY MARINE SEQUENCES, TIERRA DEL FUEGO (ARGENTINA)

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Abstract. This work is an updated review of the knowledge on the evolution and development of palaeoenvironments during the Holocene marine ingression and posterior regressive event in Tierra del Fuego. During the beginning of the marine transgression, *ca.* 8,000 cal yr BP, the vegetation in the southern coastal areas along the Beagle Channel was mainly arboreal with dominance of *Nothofagus* forest and scarcity of shrub and herbaceous communities, while in the northeastern Atlantic coast, the treeless steppe was replaced by a relatively open *Nothofagus* forest. The Early–Middle Holocene aquatic assemblages were characterized by a scarce occurrence of marine components, especially dinoflagellate cysts, suggesting the development of low energy estuarine environments with low-salinities caused by glacier meltwater discharge. After 6,000 cal yr BP, an increase in the number of aquatic species was observed with dominance of Peridiniales dinoflagellate cysts, indicating the establishment of marginal marine environments with low to moderate salinities and high nutrient levels. During the last 1,000 cal yr BP, the littoral vegetation along the Beagle Channel showed an open *Nothofagus* forest and the development of peatlands, while in the northeastern Atlantic coast the steppe vegetation developed under less humid environmental conditions related to the marine regressive event. These assemblages have a similar composition to those observed in modern sediments of the Beagle Channel and suggest palaeoenvironmental conditions comparable to today.

Key words. Palaeoenvironments. Marine sequences. Late Quaternary. Tierra del Fuego.

Resumen. REVISIÓN DE LA RECONSTRUCCIÓN PALEOAMBIENTAL DE SECUENCIAS MARINAS DEL CUATERNARIO TARDÍO, TIERRA DEL FUEGO (ARGENTINA). Este trabajo es una revisión actualizada del conocimiento sobre la evolución y desarrollo de los paleoambientes durante la ingresión marina del Holoceno y su posterior regresión en Tierra del Fuego. Durante la incursión marina *ca.* 8.000 años cal AP, la vegetación en las zonas costeras a lo largo del Canal Beagle estuvo dominada por el bosque de *Nothofagus* con escasos arbustos y hierbas, mientras que en la costa atlántica la estepa fue sustituida por un bosque de *Nothofagus* relativamente abierto. Las asociaciones acuáticas desarrolladas durante el Holoceno Temprano–Medio se caracterizaron por una escasa ocurrencia de componentes marinos, especialmente quistes de dinoflagelados, sugiriendo el desarrollo de ambientes estuarinos de baja energía y salinidad, afectados por la descarga de agua de los glaciares. Después de los 6.000 años cal AP, se observó un aumento en el número de especies acuáticas con dominancia de quistes de dinoflagelados Peridiniales, lo que sugiere el desarrollo de ambientes marinos marginales con baja a moderada salinidad y alto contenido de nutrientes. Durante los últimos 1.000 años cal AP, la vegetación litoral a lo largo del Canal Beagle mostró el predominio de un bosque abierto de *Nothofagus* y turberas, mientras que en el noreste de la costa atlántica se desarrolló una vegetación de estepa bajo condiciones ambientales menos húmedas y relacionadas al evento marino regresivo. Estas asociaciones tienen una composición similar a las observadas en los sedimentos modernos del Canal Beagle y sugiere que las condiciones paleoambientales fueron comparables a las actuales.

Palabras clave. Paleoambientes. Secuencias marinas. Cuaternario Tardío. Tierra del Fuego.

THE LATE Quaternary palynological studies, particularly of the Late Pleistocene–Holocene, represent a research line of growing interest in Argentina since they provide important information about the variability of past environments. About 15,000 years ago, the climate of the southernmost region of South America underwent irreversible transformations that determined profound changes in the geomorphology, position of the shoreline, terrestrial and coastal ecosystems of the region. The study of palaeoclimatic conditions during the last 15,000 years provides the elements to understand the history and evolution of terrestrial and marine ecosystems, their dynamics and ability to react to the climate change. The analysis of palynological organic matter preserved in the sedimentary records has special interest given its importance and potential for the palaeoenvironmental and palaeoclimatic assessment (Candel *et al.*, 2013). The palynofacies analysis comprises the study of the total palynological organic matter (palynomorphs plus other organic matter) and contributes to the understanding of marine transgressive-regressive sedimentary cycles. The relationship between the source material (continental or marine), and the size and diversity provides information on the hydrodynamics and ecology of the depositional environment (Candel *et al.*, 2013). The conventional palynological analysis considers the content of palynomorphs (pollen, spores, and organic-walled microplankton) present in a palynological preparation. The study of fossil pollen records provides evidence for the reconstruction of vegetation com-

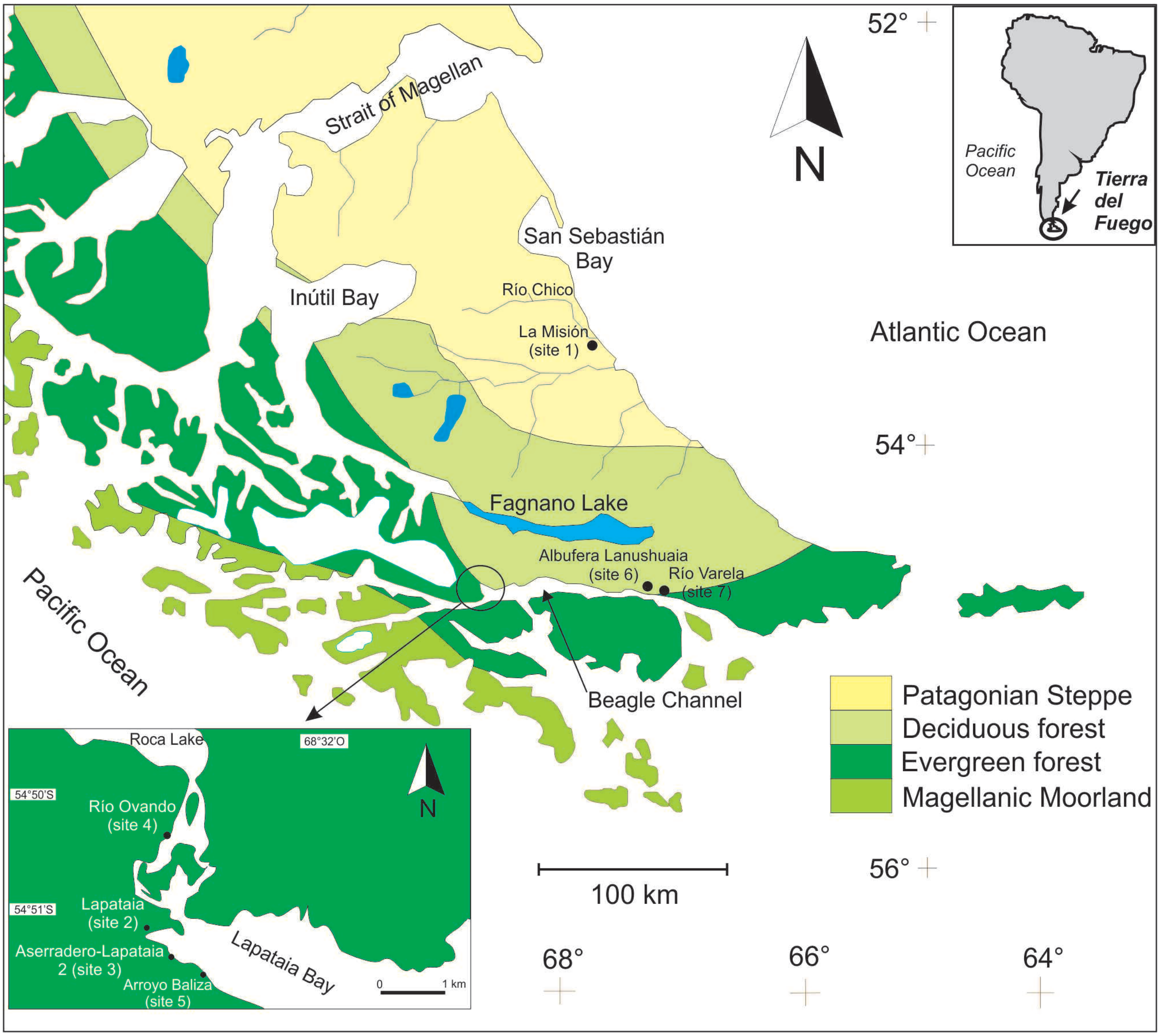


Figure 1. Vegetation map of Isla Grande de Tierra del Fuego showing the localities mentioned in the text, the vegetational units and mean annual precipitation (mm) (modified after Tuhkanen, 1992). **1,** La Misión; **2,** Lapataia; **3,** Aserradero-Lapataia 2; **4,** Río Ovando; **5,** Arroyo Baliza; **6,** Albufera Lanushuaia; **7,** Río Varela.

munities and infers the changes that occurred in these communities at spatial and temporal scales in response to environmental and climatic variations. Also, the study of marine organic-walled palaeomicroplankton (mainly dinoflagellate cysts and acritarchs) has a special interest for palaeoenvironmental assessment and palaeoclimatic inferences. Numerous studies have shown the existence of a close relationship between the distribution of dinoflagellate cyst (dinocyst) assemblages and the physico-chemical conditions of seawater such as sea-surface temperature, sea-surface salinity, nutrient availability, primary productivity and seasonality and extent of the sea ice cover (de Vernal *et al.*, 2001, 2013; Radi and de Vernal, 2008). The variations in their records are interpreted in terms of oceanographic and atmospheric changes.

Many studies of Late Quaternary palaeoecological conditions from Isla Grande de Tierra del Fuego, southernmost Patagonia, were largely based on palynological records from terrestrial sediments (Heusser and Rabassa, 1987, 1995; Heusser, 1989, 1998, 2003; Markgraf, 1993; Borromei, 1995; Quattrocchio and Borromei, 1998; Mauquoy *et al.*, 2004; Borromei *et al.*, 2007, 2010, 2014; Borromei and Quattrocchio, 2008; Markgraf and Huber, 2010; Musotto, 2013; Waldmann *et al.*, 2014; Musotto *et al.*, 2016a, in press; among others works). Studies on dinocyst assemblages and palynofacies from Late Quaternary deposits of the southern South America are still limited to a few contributions (Borromei and Quattrocchio, 2001, 2007; Grill *et al.*, 2002; Candel *et al.*, 2009, 2011, 2012, 2013, in press; Rabassa *et al.*, 2009; Candel, 2010; Candel and Borromei, 2013; Fernández *et al.*, 2014).

The present contribution is a compilation of pollen, microplankton, and palynofacies datasets from Holocene radiocarbon-dated marine deposits located in Tierra del Fuego (Tab. 1). Palaeocommunities and palaeoenvironments during the Holocene marine ingression into the Beagle Channel were interpreted from the palynological and palynofacies analyses of material mostly recovered from sites located on the northern coast of the channel. The terrace system that characterise this marine incursion into the Beagle Channel

TABLE 1. Selected Late Quaternary marine deposits from Isla Grande de Tierra del Fuego (53–55° S). The palynological sites are listed according to their location on the Atlantic coast and the northern coast of the Beagle Channel, from west to east sectors.

Site No.	*Site name*	*Latitude (S)*	*Longitude (W)*	*References*
Atlantic coast				
1	*La Misión*	*53° 30′*	*67° 50′*	*Markgraf (1980, 1993)*
North coast of Beagle Channel				
2	*Bahía Lapataia*	*54° 50′*	*68° 34′*	*Borromei and Quattrocchio (2001, 2007)*
3	*Aserradero-Lapataia2*	*54° 51′*	*68° 34′*	*Rabassa* et al. *(2009);* *Candel and Louwye (2015)*
4	*Río Ovando*	*54° 51′*	*68° 35′*	*Candel* et al. *(2009)*
5	*Arroyo Baliza*	*54° 51′*	*68° 33′*	*Candel* et al. *in press*
6	*Albufera Lanushuaia*	*54° 52′*	*67° 60′*	*Candel* et al. *(2011)*
7	*Río Varela*	*54° 52′*	*67° 11′*	*Grill* et al. *(2002)*

provides evidence for different temporal windows contributing significantly to the understanding of the palaeoenvironmental response to Holocene climate variability. Conventional radiocarbon ages of marine sediments belonging to own studies were converted to calibrated ^{14}C ages by the program Calib 7.1 (Stuiver *et al.*, 2015) using the Marine13 calibration data set (Reimer *et al.*, 2013). A local ^{14}C marine reservoir effect (ΔR) value for the study region of 221±40 years should be taken into consideration (Gordillo *et al.*, 2015). The published radiocarbon dates corresponding to marine environments and carried out by different authors have been maintained as ^{14}C ages.

GEOGRAPHICAL SETTING

Isla Grande de Tierra del Fuego is the largest island of the Fuegian Archipelago and is located at the southernmost end of South America between latitude 53–55° S and longitude 66–74° W (Fig. 1). It is the highest latitude landmass in the Southern Hemisphere outside Antarctica and is strongly influenced by the climatic conditions of the Southern Ocean and the Antarctic Peninsula. Its separation from continental South America was a result of marine flooding of deep glacial valleys during the Holocene (Rabassa *et al.*, 2011). The Beagle Channel forms a connection between the Atlantic Ocean and the Pacific Ocean in the southernmost Argentinian coast of Tierra del Fuego. It is a former tectonic valley that extends over 220 km from west to east and was completely covered by ice during the Last Glacial Maximum (LGM) *ca*. 25 ka ago (Rabassa, 2008). Following deglaciation, the depressed areas were occupied by proglacial lakes and glaciofluvial and glaciolacustrine environments until the valley was flooding by seawater (Rabassa *et al.*, 1986). The Beagle Channel opened before 8,200 ^{14}C yr BP and the lake water was replaced by seawater. The Holocene transgression is recorded at several sites along the Patagonian coast reaching a maximum sea-level between 6,500 and 4,000 yr BP (Codignotto *et al.*, 1992). According Flemming *et al.* (1998), during the period 9,500 to 7,000 yr BP the postglacial sea-level suffered a sharp rise from -24 m to -3 m indicating an uplift rate of 0.084 m/yr. The global scale of sea level rise would have accelerated around 0.428 m/yr from 7,000 BP until reach the current level.

The channel was submerged by the sea and the entire area turned into a fjord by 7,900 ^{14}C yr BP (Rabassa *et al.*, 1986) leaving marine deposits, mostly raised beaches, distributed along both the northern and southern Beagle Channel coasts (Gordillo, 1993). These deposits are mostly sandy and gravely in grain-size, although clay-like sediments are recorded mainly in the westernmost sector of the Beagle Channel. The origin of these raised beaches appears related to tectonic uplift and/or isostatic recovery following deglaciation (Rabassa *et al.*, 2000; Bujalesky *et al.*, 2004).

Conversely, the Atlantic coast was ice-free during the LGM (Rabassa *et al.*, 2000). The distinctive characteristic of the Holocene littoral deposits at the northern Atlantic coast (Bahía San Sebastián and Río Chico area) is the presence of regressive-like sequences at protected areas, while transgressive-like beach facies have developed at exposed areas (Rabassa *et al.*, 2000, p. 227). The dissimilarities in geomorphological and evolutionary trends of these littoral deposits of the northeastern Atlantic coast occurred as a consequence of the underlying palaeorelief that was dipping northwards and carved during the Pleistocene glaciations (Rabassa *et al.*, 2000). The comparison of the Holocene raised beaches between the northern Atlantic coast of Tierra del Fuego (La Misión, Río Chico, Bahía San Sebastián) (Fig. 1) and the northwestern coast of Beagle Channel (Punta Pingüinos, Bahía Golondrina, Playa Larga) (Fig. 2), indicate that these dissimilarities may partially be the result of differential tectonic uplifting rates (Rabassa *et al.*, 2000). The tectonic uplift during the last 8,000 yr was greatest at the western Beagle Channel (approximately 1.2+0.2 mm/yr), diminishing northward and eastward. It seems to be negligible toward the northern coast of Isla Grande. The glacioisostatic rebound at the Beagle Channel seems to have operated only during deglaciation or in 1–2 millennia after the final ice recession (Isla and Bujalesky, 2008).

MODERN CLIMATE AND VEGETATION

The climate of Tierra del Fuego is cold-temperate and is influenced predominantly by the seasonal shifts of the Polar Front and the cyclonic activity related to the southern westerlies (Pisano, 1977). It is highly oceanic in the western and southern parts of the archipelago and increasingly continental towards the east and north. Mean summer isotherms increase northeastward from 9 to 12 °C. The precipitation decreases to the north and east. The mean annual rainfall in Ushuaia is 570 mm and less than 300 mm in Río Grande to the north (Prohaska, 1976). The modern vegetation corresponds to the Fuego-Patagonian Steppe in the north, followed southward successively by the Subantarctic Deciduous Beech Forest and the Evergreen Beech Forest (Fig. 1). They are characterized by three species of southern beech, *Nothofagus pumilio* (Poeppig and Endl.) Krasser 1896 (lenga), *N. antarctica* (Forster f.) Oersted 1871 (ñire), and *N. betuloides* (Mirbel) Oersted 1871 (guindo), which grow to an average altitudinal limit of 550–600 m a.s.l. (meters above sea level) and predominate where precipitation exceeds 400 mm yr^{-1}. Magellanic Moorland occurs beyond the forest along the exposed outermost coast under conditions of increased precipitation, wind and poor drainage. High Andean Desert vegetation develops above the treeline (600 m a.s.l.) in the Fuegian Andes until the snowline is reached (Tuhkanen, 1992).

SURFACE SEDIMENTS SAMPLES AS MODERN ANALOGUES

Palynological and palynofacies analyses of surface sediments from the Beagle Channel (Fig. 2) were carried out to establish modern analogues for comparison with other Holocene marine records in southern Tierra del Fuego. The results showed the predominance of *Nothofagus dombeyi*-type pollen indicating the presence of forest communities in the coastal area (Candel *et al.*, 2013). The aquatic palynomorph assemblages, mainly dinoflagellate cysts, are dominated by Peridiniales over Gonyaulacales taxa (Candel *et al.*, 2012, 2013). The assemblages (Tab. 2) were mostly composed by Protoperidiniaceae such as *Brigantedinium* spp., *Echinidinium* spp., and *Selenopemphix quanta* (Bradford 1975) Matsuoka 1985, typical of a marginal marine and surface waters characterized by low to moderate salinity, and high nutrient input by rivers. These assemblages were thus compatible with the occurrence of freshwater to brackish water taxa (*Botryococcus braunii* Kützing 1849, *Botryococcus* sp., *Polyasterias* sp., *Halodinium* sp., and *Radiosperma corbiferum* Meunier 1910). The assemblages from the Beagle Channel showed similarities with those of high latitude regions of the Northern Hemisphere (Candel *et al.*, 2012).

The palynofacies showed the dominance of highly degraded translucent phytoclasts associated with amorphous organic matter (AOM) and palynomorphs, while opaque phytoclasts were poorly represented. The organic constituents indicated the proximity of a continental source area to the marine environment, with distances and/or times of relatively short transport. The predominance of translucent phytoclasts associated with pyrite suggested reducing conditions, probably associated with marginal-marine environments. The high terrestrial organic matter input into the depositional area was consistent with these coastal environments. A comparison with the sections of Holocene age (Río Varela, Aserradero-Lapataia, Arroyo Baliza, Río Ovando, and Albufera Lanushuaia) (Fig. 1) showed similar distribution of the total palynological matter (Grill *et al.*, 2002; Rabassa *et al.*, 2009; Candel *et al.*, 2011, 2013).

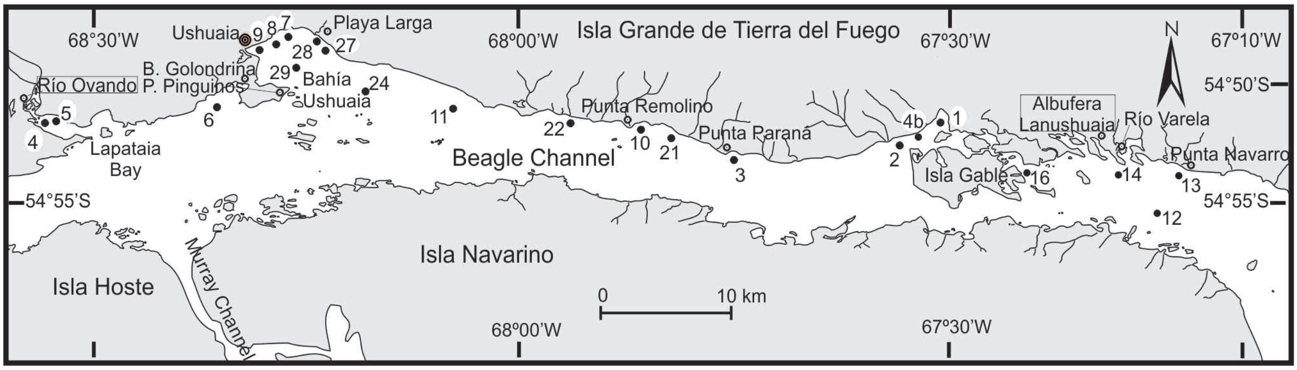


Figure 2. Detailed map of the Beagle Channel region and location of the surface sediment samples.

Table 2. Aquatic palynomorphs identified in surface sediments from the Beagle Channel area (modified after Candel *et al.*, 2012). BL, Bahía Lapataia; **BG,** Bahía Golondrina; **BU,** Bahía Ushuaia; **PR,** Punta Remolino; **PP,** Punta Paraná; **IG,** Isla Gable; **EIG,** External Isla Gable.

Sector	*WESTERN*	*CENTRAL*	*EASTERN*
Sampling sites	*BL, BG, BU*	*PR, PP*	*IG, EIG*
Dinocysts			
Brigantedinium cariacoense *(Wall 1967) Lentin and Williams 1993*		x	x
Brigantedinium simplex *Wall 1965 ex Lentin and Williams 1993*	x	x	x
Brigantedinium *spp.*	x	x	x
Dinocyst sp. 1	x	x	x
Dubridinium *cf.* **D.** *sp. Reid 1977*	x		x
Echinidinium *cf.* **E. delicatum** *Zonneveld 1997*	x	x	x
Echinidinium granulatum *Zonneveld 1997*	x	x	x
Echinidinium *cf.* **E. granulatum** *Zonneveld 1997*	x	x	x
Echinidinium *spp.*	x	x	x
Islandinium? cezare *(de Vernal* et al. *1989 ex de Vernal in Rochon* et al. *1999) Head* et al. *2001*	x	x	x
Islandinium minutum *(Harland and Reid in Harland* et al. *1980) Head* et al. *2001*	x	x	x
Pentapharsodinium dalei *Indelicato and Loeblich III 1986*	x	x	x
Polykrikos kofoidii *Chatton 1914*	x	x	x
Polykrikos schwartzii *Bütschli 1873*	x	x	x
Protoperidinioids	x	x	x
Quinquecuspis concreta *(Reid 1977) Harland 1977*	x	x	x
Selenopemphix nephroides *(Benedek 1972) Benedek and Sarjeant 1981*	x	x	x
Selenopemphix quanta *(Bradford 1975) Matsuoka 1985*	x	x	x
Selenopemphix *cf.* **S. quanta** *(Bradford 1975) Matsuoka 1985*	x	x	x
Spiniferites lazus *Reid 1974*	x		
Spiniferites ramosus *(Ehrenberg 1838) Mantell 1854 sensu lato*	x	x	x
Spiniferites *cf.* **S. mirabilis** *(Rossignol 1964) Sarjeant 1970*			x
Spiniferites *sp.*	x		
Spiniferites *spp.*	x	x	x
Trinovantedinium *cf.* **T. applanatum** *(Bradford 1977) Bujak and Davies 1983*	x	x	
Votadinium calvum *Reid 1977*	x	x	x
Votadinium spinosum *Reid 1977*	x	x	x
Dinocyst species diversity	*17*	*16*	*17*
Acritarchs			
Acritarch sp. 1		x	x
Acritarch sp. 2		x	
*?***Cyclopsiella** *sp.*		x	
Halodinium *sp.*	x	x	x
Zoomorphs			
Copepod eggs	x	x	x
Foraminiferal linings	x	x	x
Other algae			
Botryococcus braunii *Kützing 1849*	x		
Botryococcus *sp.*	x	x	x
Zygnemataceae	x		x
Spirogyra *sp.*		x	
Tasmanaceae	x		
Radiosperma corbiferum *Meunier 1910*	x	x	x
Polyasterias *sp.*	x	x	x
Other aquatic palynomorphs diversity	*8*	*10*	*8*

PALAEOENVIRONMENTS AND PALAEOCLIMATIC RECONSTRUCTION DURING THE HOLOCENE TRANSGRESSION IN TIERRA DEL FUEGO

Holocene times

The Early Holocene after 11,500 cal yr BP was characterized by a significant increase in temperature coinciding with the onset of the Antarctic Climate Optimum (Bentley *et al.*, 2009). The increasing temperature and lower levels of effective moisture than today would have favored the establishment of an open *Nothofagus* woodland in southern Tierra del Fuego (Beagle Channel area), with high fire frequency (Heusser, 1998; Markgraf and Huber, 2010); while steppe environments remained in central Tierra del Fuego (Fagnano Lake area) until *ca.* 9,500 cal yr BP (Musotto *et al.*, 2016a). Nowadays, a similar pattern of vegetation belonging to the steppe/forest ecotone and steppe is observed in the central and north sector of the island, respectively, with precipitations less than 500 mm yr^{-1} and summer temperature between 11–12 °C (Tuhkanen, 1992). This climatic scenario could have been induced by the migration of the westerlies winds toward higher latitudes, reduced Antarctic ice sheet and decrease of the thermal gradient between the poles and Ecuador (Markgraf and Huber, 2010).

This warm period was coincident with a transgressive event in Tierra del Fuego. The oldest marine levels identified into the Beagle Channel are located in the western sector: Bahía Lapataia (site 2, Fig. 1) at 8,478 cal yr BP (Rabassa *et al.*, 1986), Aserradero-Lapataia 2 (site 3, Fig. 1) at 8,408 cal yr BP (Rabassa *et al.*, 2009), and Lago Roca (Fig. 1) at 7,760 cal yr BP (Gordillo *et al.*, 1993). The ingression of marine waters generated deep and narrow fjords with complex archipelagos (Gordillo *et al.*, 1993). The Lago Roca-Lapataia area was a low energy, freshwater estuarine environment. The recorded mollusk association is represented by epibenthic taxa (mytilids and cirripeds) tolerant of estuarine conditions (Gordillo *et al.*, 1993; Gordillo, 1999). According with the mollusk assemblages, around 7,500 ^{14}C yr BP, the whole area turned into a fjord and Río Ovando (site 4, Fig. 1) and Lago Roca sites became in shallow-marine environments (Gordillo *et al.*, 2005). The mollusk assemblages indicate that the northern coast of the Beagle Channel was occupied by shallow benthic palaeocommunities during the Holocene (Gordillo, 1999; Gordillo *et al.*, 2005). Postglacial mollusk assemblages from the Beagle Channel are similar to current mollusk associations living in the region. Therefore, it was inferred that the climatic conditions remained stable enough to allow the development of these marine faunal associations with a wide ecological range (Gordillo, 1999).

In the northeastern Atlantic coast at the La Misión locality (site 1, Figs. 1 and 7), a sediment core located circa 3.5 km from the present shore, holds marine sediments dated between 8,720 ^{14}C yr BP and 270 ^{14}C yr BP (Markgraf, 1983, 1993). Changes in Chenopodiaceae pollen, diatoms and ostracodes provided a history of the sea-level variation. The marine sediments are clays with high percentages of Chenopodiaceae pollen and an abundance of diatom and ostracode taxa with brackish to coastal marine affinities (Markgraf, 1980, 1993). During the marine transgression, the vegetation was represented by a relatively open *Nothofagus* forest at *ca.* 8,000 ^{14}C yr BP. This forest environment continued with only minor changes until after 1,000 ^{14}C yr ago, when the steppe expanded again (Markgraf, 1993).

Early to Mid-Holocene marine palynomorph assemblages

Between *ca.* 8,200 and 5,500 cal yr BP the palynological analysis showed for the Bahía Lapataia locality in western the Beagle Channel (site 2, Figs. 3 and 7) the presence of marginal-marine environments with a predominance of terrestrial palynomorphs over marine palynomorphs indicating an important freshwater input. Two relatively higher sea levels were identified by the increased abundance of marine palynomorphs; the first was observed between 8,478 cal yr BP and the second after 5,978 cal yr BP (Borromei and Quattrocchio, 2007). The marine palynomorphs were characterized by a poor dinoflagellate cyst assemblage dominated by Peridiniales taxa (*Brigantedinium* spp. and *Selenopemphix* sp.) over Gonyaulacales taxa (*Spiniferites* spp. and *Operculodinium centrocarpum* Deflandre and Cookson 1955 *sensu* Wall 1967) (Fig. 6). The acritarch *Halodinium* sp. and zoomorphs, such as foraminiferal linings and copepod eggs, were abundant. This marine palynomorph assemblage reflects an inner estuarine environment with low and variable salinities and/or turbulence, cool-temperate sea water temperature and abundance of dissolved nutrients caused by freshwater runoff (Borromei and Quattrocchio, 2001, 2007). Likewise, the palynological record from Aserradero-Lapataia 2 (site 3) showed at 8,408 cal yr BP a dominance of arboreal *Nothofagus* pollen associated with shrubs and herbs. The aquatic palynomorph assemblage consisted of dinoflagellate cysts (mainly *Brigantedinium simplex* Wall 1965 ex Lentin and Williams 1993, *Echinidinium granulatum* Zonneveld 1997, *Selenopemphix quanta*, *Polykrikos schwartzii* Bütschli 1873, among others) which showed an increasing diversification from the middle to upper part of the section, acritarchs (*Halodinium* sp., *Palaeostomocystis fritilla* Bujak 1984, and *P. subtilitheca* Roncaglia 2004), foraminiferal linings, copepod eggs and freshwater to brackish-marine algae (Candel and Louwye, 2015). The low dinoflagellate cyst species diversity could indicate the development of low-salinity environments affected by glacier meltwater discharge. These environments persisted at least several years, as the influence of seawater was expanding by global eustatic rise (Candel and Louwye, 2015).

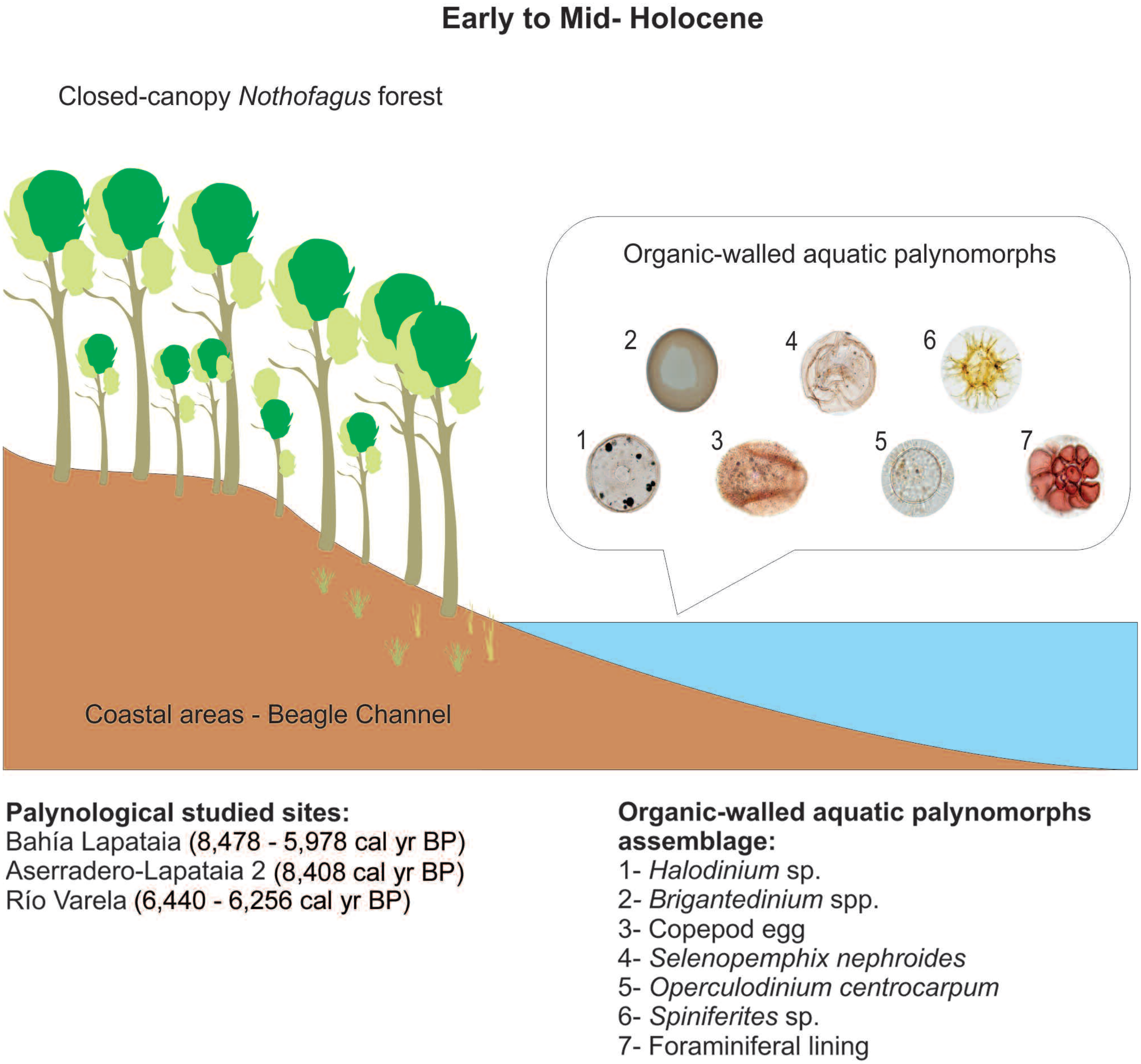


Figure 3. Evolutionary coastal model during the Early and Mid-Holocene of the Beagle Channel.

East of Beagle Channel, more precisely at Río Varela locality (site 7, Figs. 1, 3 and 7) 100 km to the east of Bahía Lapataia site, two marine levels were identified. The first level was recorded at the base of the sequence at 6,440 cal yr BP (Units 1-2: 1.60 m depth), and the other marine level at 6,256 cal yr BP (Unit 4: 1.27 m depth) (Grill *et al*., 2002). Unit 1 holds a microplankton assemblage constituted by Protoperidiniaceae dinocysts (*Brigantedinium* spp. and *Selenopemphix nephroides* (Benedek 1972) Benedek and Sarjeant, 1981), the acritarch *Halodinium* sp., copepod eggs and foraminiferal linings. These palynomorphs indicated a nearshore and low-energy environment with high nutrients supply, low salinity and cooler sea water temperature. In Unit 2 the record of Gonyaulacales dinocysts (*Spiniferites* sp. and *Operculodinium centrocarpum;* Fig. 6), accompanied with a decrease in *Halodinium* sp. and zoomorphs, suggested external neritic-marine conditions. Towards 6,256 cal yr BP (Unit 4) the presence of heterotrophic dinocysts (*Brigantedinium* spp. and *Selenopemphix nephroides*), *Halodinium* sp., and foraminiferal linings indicating a marine environment with nutrient-rich waters, variable salinity and high fluvial input (Grill *et al*., 2002). The organic matter content in sediments from Río Varela was mainly characterized by amorphous organic matter (AOM) related to degraded plankton and associated with pyrite, indicating anoxic marine conditions (Grill *et al*., 2002).

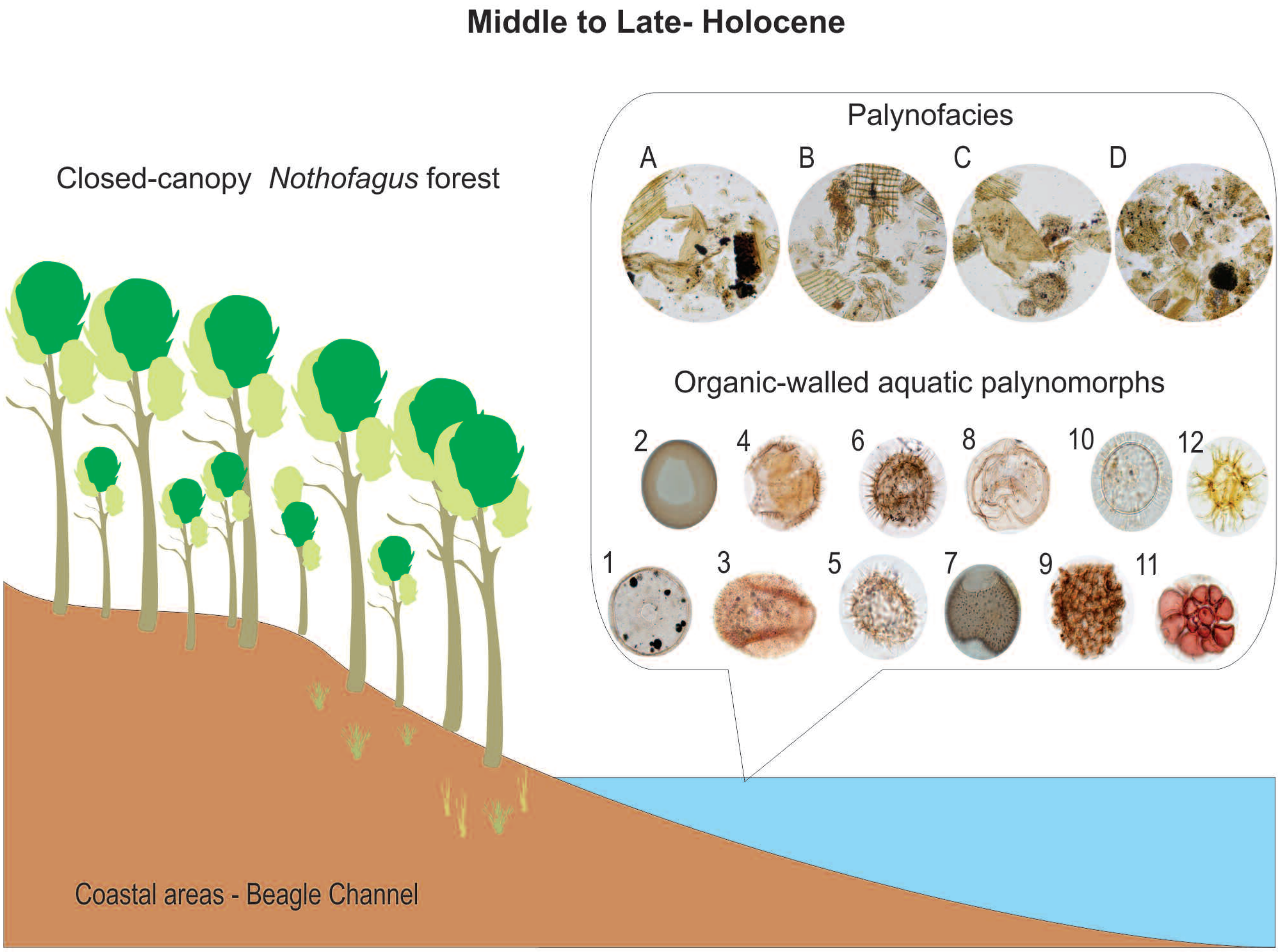
The pollen records revealed in coastal areas, prior to the transgressive event, the development of the forest-steppe ecotone in concordance with the regional vegetational pattern (Borromei and Quattrocchio, 2008). However, at the time of the marine incursion the coastal vegetation in the Beagle Channel area was mainly arboreal characterised by a significant increase in *Nothofagus* pollen, suggesting high effective moisture due to the moderating action of the sea (Grill *et al*., 2002; Borromei and Quattrocchio, 2007, 2008).

Middle to Late Holocene marine palynomorph assemblages

The climate changed towards colder and wetter conditions after *ca*. 6,000 cal yr BP, and favored the regional expansion of a closed-canopy *Nothofagus* forest, the replacement of minerotrophic fens to ombrotrophic *Sphagnum* bogs, and the decrease in fire activity (Heusser, 2003; Markgraf and Huber, 2010; Musotto *et al*., 2016a, in press). In coastal areas, significant percentages of *Nothofagus* pollen recorded throughout the profiles suggested the presence of a closed-canopy forest, confirming the existence of a cool and wet climate (Candel *et al*., 2009, in press). These climatic conditions could be related with the increased strength and enhanced seasonal cycle of the westerlies (Markgraf and Huber, 2010).

Low concentration and diversity of dinocysts (9 identified taxa) were recorded in the eastern sector of Beagle Channel, at Albufera Lanushuaia (site 6, Figs. 1, 4 and 7). Between 5,916 cal yr BP and 5,713 cal yr BP, the dinocysts assemblage showed low diversity species (*Brigantedinium* spp., *Echinidinium* spp., *Islandinium minutum* (Harland and Reid in Harland *et al*., 1998) Head *et al*. 2001, *Dubridinium* sp. Reid 1977, *Selenopemphix nephroides*, round brown cysts, and indeterminate proximochorate dinocysts) suggested a marginal-marine environment with low to moderate salinity and high nutrients concentration in the surface waters, probably due to the contribution of freshwater runoff. After 5,713 cal yr BP, a slight increase in species diversity and a decrease in the concentration of the dinocysts were observed. The assemblage included *Brigantedinium* spp., *Echinidinium* spp., *Selenopemphix quanta, Selenopemphix* cf. *S. quanta*, *Votadinium spinosum* Reid 1977, *Polykrikos kofoidii* Chatton 1914, *Polykrikos schwartzii*, round brown cysts, and indeterminate proximochorate dinocysts (Fig. 6). The assemblage suggested environmental conditions similar to the beginning of this sedimentary sequence. However, the presence of species such as *P. kofoidii*, *P. schwartzii,* and *V. spinosum* could indicate a marine environment with normal salinity above 30 psu (Candel, 2010; Candel *et al*., 2011). The palynofacies analysis showed a dominance of translucent phytoclasts accompanied by amorphous organic matter and palynomorphs. Thus, the organic constituents indicated the proximity of a continental source to the marine environment, with relatively short distances and/or times of transport. The predominance of translucent phytoclasts associated with pyrite suggested reducing conditions, probably related to marginal-marine environments (Candel *et al*., 2011).

At the western sector of the Beagle Channel, the palynological analysis of Río Ovando (site 4, Figs. 4, 7) showed the dominance of terrestrial (pollen grains and spores) over aquatic palynomorphs (dinocysts, acritarchs, foraminiferal linings, copepod eggs and other algae) during the Middle Holocene. Towards 3,929 cal yr BP, a relatively high species diversity of 10 identified taxa and a low concentration of dinocysts were recorded. The identified dinocysts assem-



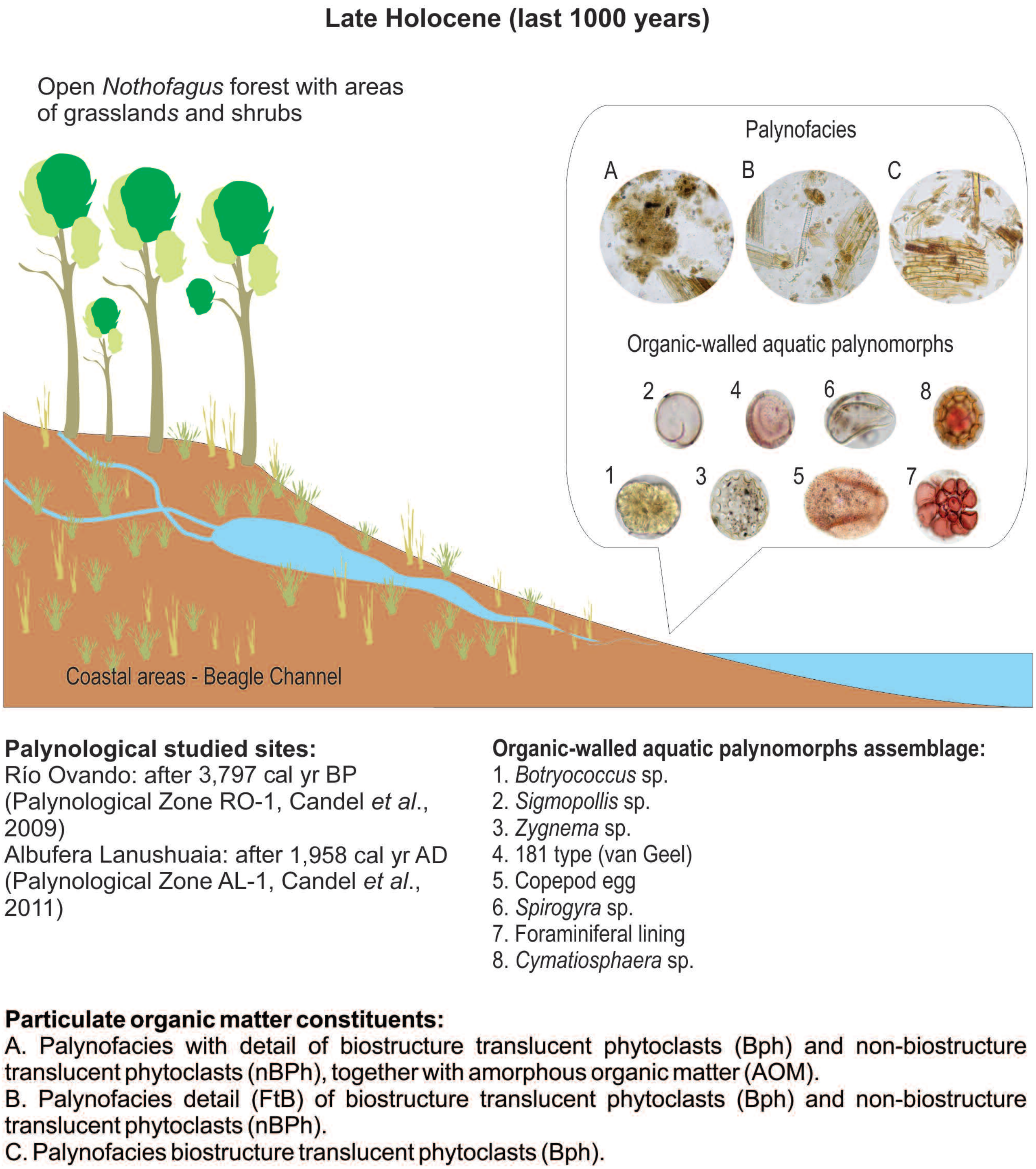
Palynological studied sites:
Albufera Lanushuaia: 6,000 - 5,713 cal yr BP
Río Ovando: 3,929 - 3,797 cal yr BP
Arroyo Baliza: 3,499 - 2,595 cal yr BP

Particulate organic matter constituents:
A-B. Palynofacies with detail of biostructure translucent phytoclasts (BPh) and non-biostructure translucent phytoclasts (nBPh), palynomorphs (Pollen) and pyrite (Py).
C-D. Palynofacies with detail of non-biostructure translucent phytoclasts (nBPh), amorphous organic matter (AOM) and dinocysts (D).

Organic-walled aquatic palynomorphs assemblage:
1- *Halodinium* sp.
2- *Brigantedinium* spp.
3- Copepod egg
4- *Islandinium minutum*
5- *Echinidinium granulatum*
6- *Selenopemphix quanta*
7- *Votadinium spinosum*
8- *Selenopemphix nephroides*
9- *Polykrikos schwartzii*
10- *Operculodinium* cf. *O. centrocarpum*
11- Foraminiferal lining
12- *Spiniferites* sp.

Figure 4. Evolutionary coastal model during the Middle and Late Holocene of the Beagle Channel.

blage (*Islandinium minutum*, *Islandinium* cf. *I. minutum*, *Echinidinium* spp., accompanied by *Brigantedinium* spp., *Polykrikos kofoidii*, *Polykrikos schwartzii*, *Operculodinium* cf. *O. centrocarpum*, and *Selenopemphix quanta*) (Fig. 6) suggested a marginal-marine environment with low to moderate salinity and high concentrations of nutrients in the sea surface waters,

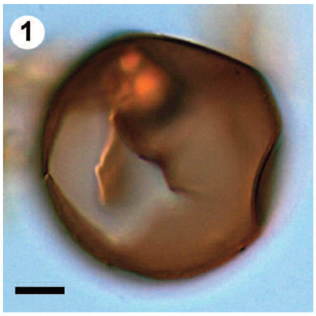


Palynological studied sites:
Río Ovando: after 3,797 cal yr BP (Palynological Zone RO-1, Candel *et al.*, 2009)
Albufera Lanushuaia: after 1,958 cal yr AD (Palynological Zone AL-1, Candel *et al.*, 2011)

Organic-walled aquatic palynomorphs assemblage:
1. *Botryococcus* sp.
2. *Sigmopollis* sp.
3. *Zygnema* sp.
4. 181 type (van Geel)
5. Copepod egg
6. *Spirogyra* sp.
7. Foraminiferal lining
8. *Cymatiosphaera* sp.

Particulate organic matter constituents:
A. Palynofacies with detail of biostructure translucent phytoclasts (Bph) and non-biostructure translucent phytoclasts (nBPh), together with amorphous organic matter (AOM).
B. Palynofacies detail (FtB) of biostructure translucent phytoclasts (Bph) and non-biostructure translucent phytoclasts (nBPh).
C. Palynofacies biostructure translucent phytoclasts (Bph).

Figure 5. Evolutionary coastal model during the last 1,000 years of the Beagle Channel.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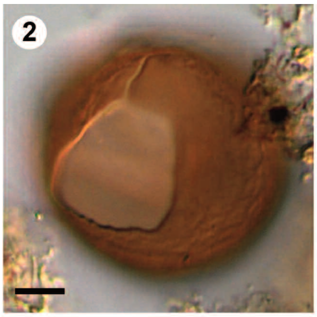
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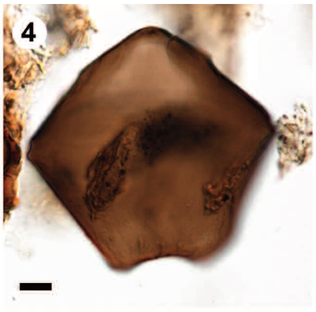
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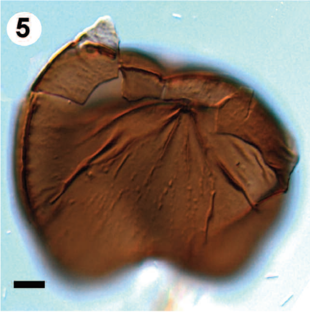
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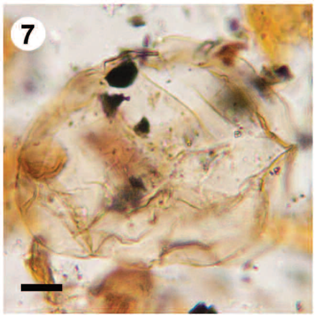
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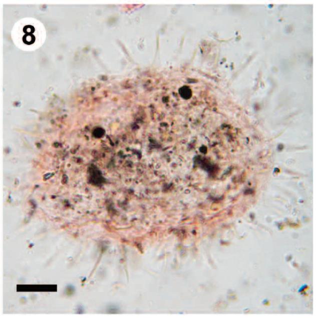
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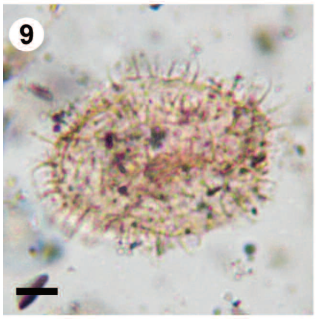
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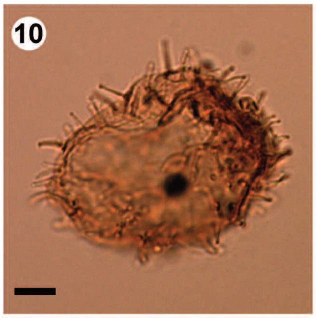
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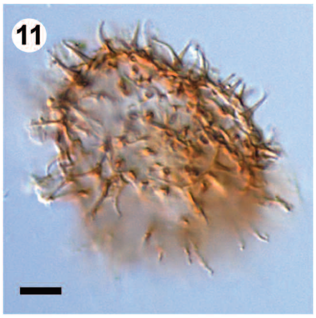
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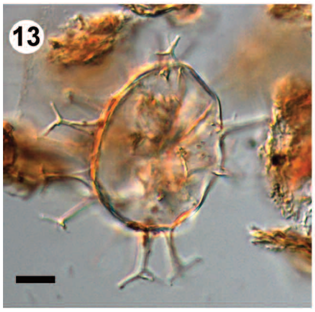
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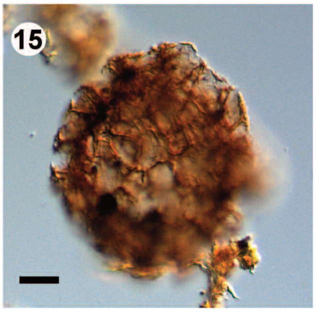
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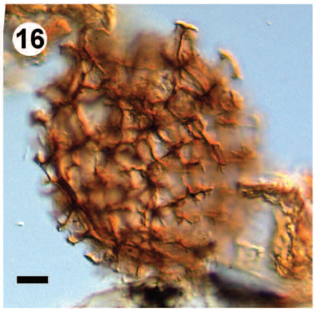
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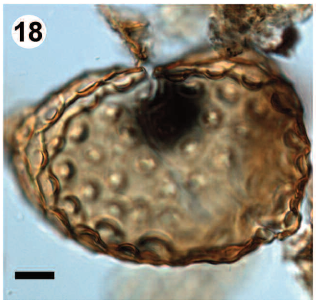
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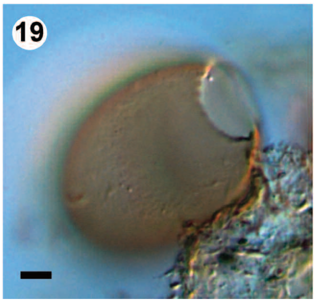
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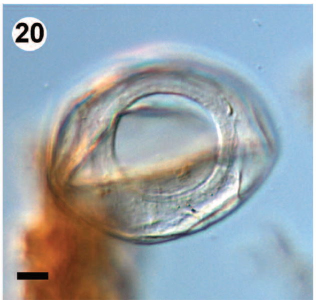
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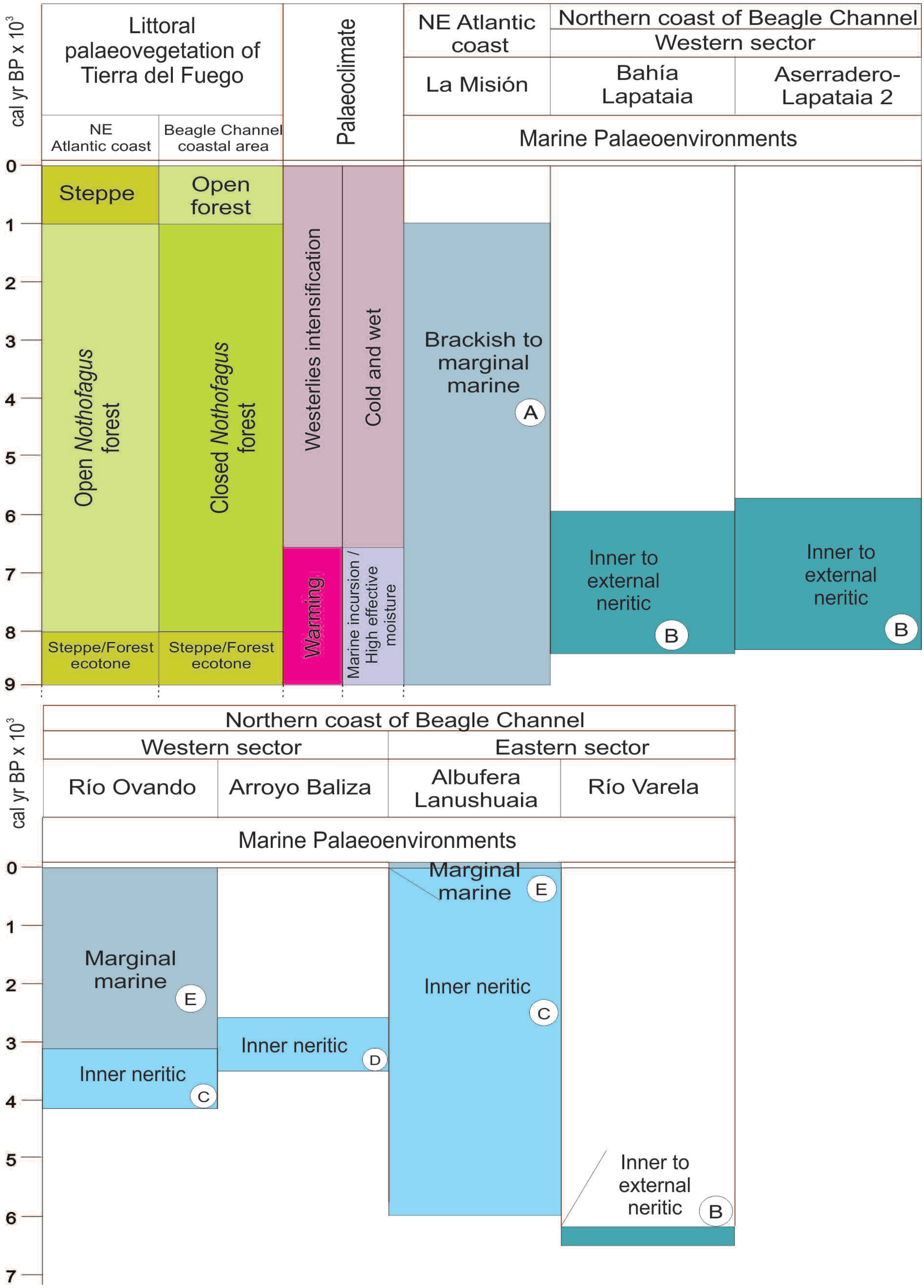
probably due to the contribution of freshwater by runoff (Candel, 2010). This diversification of species was also supported by data from mollusks confirming that during this period a major expansion took place of the fauna through a diversification of mollusk assemblages characterized by *Tawera gayi*, *Venus antiqua*, *Hiatella solida*, *Trophon geversianus*, *Xymenopsis muriciformis*, *Pareuthria plumbea*, *Laevilitorina*, *Neolepton*, *Carditella naviformis*, and *Cyclocardia compresa*. This indicates a change to present-day conditions. Most of these species could have survived the neoglacial episodes (Gordillo *et al.*, 2005). A dinocysts assemblage dominated exclusively by *Islandinium-Echinidinium* complex was recorded between 3,929 and 3,797 cal yr BP, showing the greatest abundance but lower diversity of dinocysts. This assemblage might indicate the occurrence of 'opportunistic species' suggesting a high input of freshwater by surface runoff. The low diversity of microplankton associations may be indicative of stressed, restricted conditions with often unstable salinities (Gorin and Steffen, 1991). According to Sluijs (2006), the sediments deposited under low-oxygen conditions show reduced cyst diversities and high abundance of a single species. The low dinoflagellate production suggested by the sparse dinocyst occurrences may be related to low and variable salinities and/or turbulence which inhibits dinoflagellate production (de Vernal and Giroux, 1991). At the same time, the replacement of a varied mollusk assemblage, characterized by venerids and other bivalves including mollusks, gastropods and chitons, by an almost monospecific assemblage (*Mytilus* Hupé in Gay 1854 and *Hiatella* Sowerby 1834) tolerant to low or variables salinities suggested a high seasonal freshwater input by river discharge and/or glacial meltwater (Candel *et al.*, 2009). The interval between 3,797 and 3,164 cal yr BP was characterized by an increase of the species diversity and a decrease of the dinocysts concentration. The assemblage composed by *Echinidinium granulatum, Echinidinium delicatum* Zonneveld 1997*, Echinidinium* spp., *Islandinium minutum*, accompanied by *Selenopemphix* spp., *Brigantedinium simplex,* cf. *Pentapharsodinium dalei*, and *Spiniferites* spp., suggested environmental conditions comparable with those at the beginning of the sequence (Candel *et al.*, 2009; Candel, 2010). The palynofacies analysis of Río Ovando showed high frequencies of mostly translucent phytoclasts associated with sporomorphs and freshwater algae, suggesting high fluvial input into the marine environment with relatively short distances and/or times of transport, related to the proximity of a terrestrial source. Also, these samples showed low percentages of AOM content suggesting oxic to dysoxic conditions in the depositional environment with good to moderate bottom water ventilation (Roncaglia, 2004; Candel, 2010; Candel *et al.*, 2013).

In the same sector of the channel, the Arroyo Baliza section (site 5, Figs. 1, 4 and 7) (3,499–2,595 cal yr BP) is located closer to the previous locality (site 4), although with a more open geographic setting influenced by the open seawaters of the Beagle Channel. Consequently, the record from this section show that aquatic palynomorphs are represented by 18 dinoflagellate cyst taxa (mainly *Brigantedinium simplex*, *Brigantedinium* spp., *Polykrikos schwartzii*, *Echinidinium granulatum*, *Dubridinium* sp., *Polykrikos kofoidii*, *Selenopemphix nephroides*, *S. quanta* and *Islandinium cezare* (de Vernal *et al*. 1989 ex de Vernal in Rochon *et al*. 1999) Head *et al*., 2001. The acritarchs *Halodinium* sp., *Palaeostomocystis fritilla, P. subtilitheca* and *P.* sp1 (Fig. 6) are also

Figure 6. Photomicrographs of the main aquatic palynomorphs identified in fossil marine sediments from the Beagle Channel. Scale bar is 10 µm. Sample number followed by England Finder coordinates. **1,** ***Brigantedinium cariacoense*****, LGC AB25-B25/2** (in Candel *et al.*, in press); **2,** ***Brigantedinium simplex*****, LGC AB9-A33/2**; **3,** ***Dubridinium*** sp., **LGC AB22-S20/3** (in Candel *et al.*, in press); **4,** ***Quinquecuspis concreta*****, LGC AB5-P35/4** (in Candel *et al.*, in press); **5,** ***Votadinium calvum*****, LGC AB21-V25** (in Candel *et al.*, in press); **6,** ***Votadinium spinosum*****, UNSP AL2638-Q47/4** (in Candel and Borromei, 2013); **7,** ***Selenopemphix nephroides,*** **UNSP BL1631a-C22/2** (in Candel and Borromei, 2013), **8,** ***Selenopemphix quanta,*** **UNSP RO1972b-M38/2** (in Candel *et al.*, 2009); **9,** ***Islandinium minutum,*** **UNSP RO1968-S14/2** (in Candel and Borromei, 2013); **10,** ***Islandinium cezare*****, LGC AB18-U20/1** (in Candel *et al.*, in press); **11,** ***Echinidinium granulatum*****, LGC AB11-W41** (in Candel *et al.*, in press); **12,** ***Operculodinium centrocarpum*****, UNSP RV1532a-F23/3** (in Candel and Borromei, 2013); **13,** ***Spiniferites ramosus*****, LGC AB1-Q24/4** (in Candel *et al.*, in press); **14,** ***Spiniferites*** sp., **UNSP BL843a-K53** (in Candel and Borromei, 2013); **15,** ***Polykrikos kofoidii*****, LGC AB4-M34/4** (in Candel *et al.*, in press); **16,** ***Polykrikos schwartzii*****, LGC AB4-O13** (in Candel *et al.*, in press); **17,** ***Halodinium*** sp., **UNSP RO1972c-R13** (in Candel *et al.*, 2009); **18,** ***Zygnema*** sp., **LGC AS19-H15/3**; **19,** ***Palaeostomocystis fritilla,*** **LGC AB12-J25/2**; **20,** ***Palaeostomocystis subtilitheca*****, LGC AB10-H11/1** (in Candel *et al.*, in press).


cal yr BP x 10^3
Littoral palaeovegetation of Tierra del Fuego
NE Atlantic coast
Beagle Channel coastal area
Palaeoclimate
NE Atlantic coast
Northern coast of Beagle Channel
Western sector
La Misión
Bahía Lapataia
Aserradero-Lapataia 2
Marine Palaeoenvironments
0
1
2
3
4
5
6
7
8
9
Steppe
Open forest
Open Nothofagus forest
Closed Nothofagus forest
Steppe/Forest ecotone
Steppe/Forest ecotone
Westerlies intensification
Cold and wet
Warming
Marine incursion / High effective moisture
Brackish to marginal marine
A
Inner to external neritic
B
Inner to external neritic
B
cal yr BP x 10^3
Northern coast of Beagle Channel
Western sector
Eastern sector
Río Ovando
Arroyo Baliza
Albufera Lanushuaia
Río Varela
Marine Palaeoenvironments
0
1
2
3
4
5
6
7
Marginal marine
E
Inner neritic
C
Inner neritic
D
Marginal marine
E
Inner neritic
C
Inner to external neritic
B

present together with foraminiferal linings, copepod eggs and freshwater to brackish-marine algae (*Zygnema* sp., *Spirogyra* sp., *Cymatiosphaera* sp., *Tasmanites* sp.). The palynological records from the Arroyo Baliza site have a similar composition to those observed in surface samples from the Beagle Channel (Candel *et al*., 2012), with a higher diversity of dinoflagellate cyst species, suggesting that the environmental conditions during the late Holocene are comparable to today. It indicates that most of the marine species were able to persist in the area even during neoglacial climatic deterioration (Candel *et al*., in press). A preliminary palynofacies analysis of Arroyo Baliza showed a dominance of translucent phytoclasts, mainly non-structured, degraded and pale in colour, with some of them in transition to amorphous organic matter (Rabassa *et al*., 2009). The high numbers of translucent phytoclasts indicate the proximity of a continental source to the marine depositional environment and thus a relatively short transportation time.

Late Holocene marine palynomorph assemblages

Palaeoclimatic records from southern South America during the last 1,000 cal yr BP, indicate a general trend of decreasing temperature (reduced insolation) and an increase in the westerly winds intensity, culminating with the Little Ice Age event (*ca.* 600–100 yr BP) (Moy *et al*., 2009). Marine records from the Chilean continental shelf (41°S) show cooling surface seawater temperature about ~1.5° C (Lamy *et al*., 2001) and ~1° C (Mohtadi *et al*., 2007) from 2,000 cal yr BP culminating in the last 100 years, probably due to the northward shift in the Antarctic Circumpolar Current and the westerly winds (Moy *et al*., 2009).

The uppermost section in Río Ovando (site 4, Figs. 5 and 7) recorded a decrease in the *Nothofagus* and an increase in grass and shrub associated with an increase of Prasinophyceae (*Cymatiosphaera* (Wetzel) Deflandre 1954) and Zygnemataceae (*Spirogyra* Link 1820) algae. This palynomorph assemblage suggested the development of an open *Nothofagus* forest with areas of grassland and shrubs, with river discharge to the marine environment indicated by the occurrence of freshwater to brackish aquatic palynomorphs related to a sea-level regressive event (Candel, 2010).

On the other hand, eastwards in Beagle Channel, at Albufera Lanushuaia (site 6, Figs. 5 and 7) showed similar conditions after 1958 cal yr AD to those observed in the uppermost section of Río Ovando. The development of an open forest of *Nothofagus* is accompanied with an increase in herb-shrub vegetation and by an increase in copepod eggs and foraminiferal linings reflecting the proximity of marine environments (Candel *et al*., 2011).

FINAL REMARKS

The Early Holocene climatic amelioration, following by a deglaciation, was accompanied by a marine transgression in Tierra del Fuego. During the marine incursion the vegetation in the coastal areas along the Beagle Channel was mainly arboreal with a dominance of a *Nothofagus* forest and scarcity of shrub and herbaceous communities indicative of high effective moisture conditions caused by the moderating action of the sea. Also, in the northeastern Atlantic coast the treeless steppe was replaced by a relatively open *Nothofagus* forest at times of the Holocene marine transgression. The cold and wet conditions during the Middle to Late Holocene favored the regional expansion of a closed-canopy *Nothofagus* forest. During the last 1,000 years BP, the littoral vegetation along the Beagle Channel

Figure 7. Palaeoenvironmental correlation of the Holocene marine deposits from Tierra del Fuego. **A,** Diatoms: ***Melosira sulcata***, ***Actinoptychus undulatus***, ***Hyalodiscus***. Ostracodes: ***Loxoreticulatum fallax, Loxocythere*** sp., ***Cytherura***, ***Cytheromorpha***, ***Perissocytheridea***. **B,** Organic-walled dinocyst assemblage: ***Brigantedinium*** spp., ***Selenopemphix nephroides***, ***S. quanta***, ***Polykrikos schwartzii***, ***Spiniferites*** sp., ***Operculodinium centrocrapum.*** **C,** Organic-walled dinocyst assemblage: ***Brigantedinium*** spp., ***Islandinium minutum***, ***Echinidinium*** spp., ***Selenopemphix nephroides***, ***S. quanta***, ***Votadinium spinosum***, ***Polykrikos kofoidii***, ***P. schwartzii***, cf. ***Pentapharsodinium dalei,*** cf. ***Dubridinium*** sp. **D,** Organic-walled dinocyst assemblage: ***Brigantedinium cariacoense***, ***B. simplex***, ***Dubridinium caperatum***, ***Echinidinium delicatum***, ***E. granulatum***, ***Islandinium cezare***, ***I. minutum***, cyst of ***Pentapharsodinium dalei***, ***Polykrikos schwartzii***, ***P. kofoidii***, ***Quinquecuspis concreta***, ***Selenopemphix nephroides***, ***S. quanta***, ***Trinovantedinium applanatum***, ***Votadinium calvum***, ***V. spinosum***, ***Operculodinium centrocarpum***, ***Spiniferites ramosus***. **E,** Aquatic palynomorphs assemblage: foraminiferal linings, copepod eggs, Prasinophyceae and Zygnemataceae.

coast was characterised by an open *Nothofagus* forest and the development of peatlands, while in the northeastern Atlantic coast the steppe vegetation developed under less humid environmental conditions related to a regressive event.

The Holocene marine sediments were characterized by marine palynomorph assemblages dominated by Peridiniales taxa that suggested the development of low energy estuarine environments with low-salinities due to glacier meltwater discharge. These environments would have persisted as the influence of seawater was expanding by global eustatic rise. The increasing salinity was accompanied by an increase in biodiversity in both dinoflagellate cysts and mollusks assemblages.

The marine assemblages recorded in the Middle and Late Holocene sediments (Albufera Lanushuaia, Río Ovando, and Arroyo Baliza sites) showed greater species diversity of dinocysts than those identified in the marine deposits of Early to Mid-Holocene age (Bahía Lapataia and Río Varela sites). This species diversification suggests an increase in marine palaeoproductivity caused by the input of terrigenous nutrients by water runoff probably related to a precipitation increase. Palaeoclimatic evidence from Tierra del Fuego show an increase in precipitation after *ca*. 6,000 yr BP caused by an intensification and/or latitudinal migration of the Westerlies (Markgraf and Huber, 2010).

The Late Holocene marine assemblages have a similar composition to those observed in the surface samples from the Beagle Channel. A higher diversity of dinocyst species was observed in comparison to the Early Holocene assemblages, suggesting palaeoenvironmental conditions comparable to today in the Beagle Channel. Probably, most of the marine species were able to persist in the area even during minor climatic fluctuations.

The palynofacies analysis indicates continental supply to marine environments coming from nearby sectors, and without significant transport. The dominance of translucent phytoclasts associated with pyrite suggests reducing conditions, probably related to marginal-marine environments. Also, high frequencies of AOM indicate the proximity of a terrestrial source with high organic matter input into the aquatic environment combined with favorable conditions for bacterial action.

ACKNOWLEDGEMENTS

This work is dedicated to Prof. Dr. Mirta Elena Quattrocchio, who the authors considered as their “scientific mother”. We would like to give a special tribute to Mirta for being a figurehead woman in the field of Argentinian Palynology, a model for generations of young Palynologists in Argentina (and elsewhere), especially in marine and terrestrial studies of Mesozoic and Cenozoic. The authors are also grateful to Marcelo A. Martínez and Lorena L. Musotto (INGEOSUR-CONICET, Universidad Nacional del Sur, Argentina), Juan Federico Ponce and Andrea Coronato (CADIC-CONICET, Ushuaia, Argentina) for field assistance and contributing resources in the field work. We thank Marcelo A. Martínez and Daniela E. Olivera for invited us to contribute to this volume and for their editorial support, and also to two reviewers for their constructive comments that helped to improve our manuscript. This paper was funded by grants PIP 11220100100041 (CONICET) and PGI 24/H126 (Secretaría General de Ciencia y Tecnología, UNS).

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LATE CENOZOIC VERTEBRATES FROM THE SOUTHERN PAMPEAN REGION: SYSTEMATIC AND BIO-CHRONOSTRATIGRAPHIC UPDATE

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Abstract. The knowledge of the vertebrate systematics and bio-chronostratigraphy of Late Cenozoic from the southwest of the Buenos Aires Province is updated. The study is focused on 12 localities that encompass the latest Miocene to the Holocene. Biostratigraphic units were identified and correlated to those of other areas of the Pampean Region. Farola Monte Hermoso, Bajo San José and Playa del Barco outstand because they yielded a large amount of fossil remains. In turn, the quarries near Grünbein allowed refining the age of "Huayquerian" faunas and their relationship with "Montehermosan" ones. The localities Cantera Seminario, Barrancas de Sarmiento, Cantera Vialidad, and Cantera Relleno Sanitario are assigned to the latest Miocene-earliest Pliocene; Farola Monte Hermoso and Las Oscuras, to the Early Pliocene; Bajo San José to the Middle Pleistocene; Puesto La Florida, Chacra Santo Domingo, and García del Río to the Late Pleistocene–Holocene; Playa del Barco to the Late Pleistocene; Pliocene *s.l.,* and Pleistocene–Holocene levels are exposed at Balneario Saldungaray.

Key words. Biostratigraphy. Mammals. Late Miocene–Holocene. Buenos Aires Province. Argentina.

Resumen. VERTEBRADOS DEL CENOZOICO TARDÍO DEL SUDOESTE DE LA REGIÓN PAMPEANA: ACTUALIZACIÓN SISTEMÁTICA Y BIO-CRONOESTRATIGRÁFICA. Se realiza una actualización del conocimiento de la sistemática de los vertebrados y la bio-cronoestratigrafía del Cenozoico tardío del sudoeste de la Provincia de Buenos Aires. El trabajo se enfoca en 12 localidades que abarcan desde el Mioceno más tardío hasta el Holoceno. En ellas se identificaron unidades bioestratigráficas que se correlacionan con otras áreas de la Región Pampeana. Se destacan Farola Monte Hermoso, Bajo San José y Playa del Barco como las localidades más fosilíferas. Por su parte, las canteras cercanas a la localidad de Grünbein se destacan por permitir la aproximación a las edades de faunas "huayquerienses" y su relación con las "montehermosenses". Las localidades Cantera Seminario, Barrancas de Sarmiento, Cantera Vialidad y Cantera Relleno Sanitario se asignan al Mioceno más tardío–Plioceno más temprano; Farola Monte Hermoso y Las Oscuras al Plioceno Temprano; Bajo San José al Pleistoceno Medio; Puesto La Florida, Chacra Santo Domingo y García del Río al Pleistoceno Tardío–Holoceno; Playa del Barco al Pleistoceno Tardío; en Balneario Saldungaray afloran niveles asignados al Plioceno *s.l.* y al Pleistoceno–Holoceno.

Palabras clave. Bioestratigrafía. Mamíferos. Mioceno Tardío–Holoceno. Provincia de Buenos Aires. Argentina.

THE TEMPORAL scheme of the South American Cenozoic was established in the XIX Century by Ameghino (*e.g.*, Ameghino, 1889, 1898) on the basis of mammal assemblages of Patagonia and central Argentina. Pascual *et al.* (1965) introduced the first scheme of South American land-mammal ages (SALMAs), following the proposal of Ameghino, which was not substantially modified. The temporal calibration of the continental Late Miocene–Holocene is based mostly on mammal faunas from central Argentina. This interval includes the Chasicoan, Huayquerian, Montehermosan, Chapadmalalan, Marplatan, Ensenadan, Bonaerian, Lujanian and Platan SALMAs and Stages/Ages (Cione and Tonni, 1995, and references therein).

The southwestern Buenos Aires Province represents an outstanding area to study the biochronology and biostratigraphy of this interval based on the analysis of mammals because it has several outcrops bearing remains of at least the last 10 My. Some of them were already well known in the paleontological literature, for example Farola Monte Hermoso (Darwin, 1846; Bravard, 1857; Ameghino, 1887, 1889; Frenguelli, 1928, 1950; J.L. Kraglievich, 1946; Leanza, 1948; Bonaparte, 1960; more recently Tonni *et al.*, 1992, among others), Punta Alta (Darwin, 1846), Playa del Barco (Ameghino, 1908; L. Kraglievich, 1926, 1934; Frenguelli, 1928; Cabrera, 1929; J.L. Kraglievich, 1946; Parodi Bustos, 1962; more recently Aramayo and Manera de Bianco, 1989; Tomassini *et al.*, 2010). However, the idea to undertake investigations with a multidisciplinary approach began in the 1980s with the initiative of Dr. Mirta Quattrocchio by forming a team to conduct geo-paleontological researches.

The Laboratory of Palynology of the Universidad Nacional del Sur headed by Dr. Quattrocchio was already well known for the palynological studies in Argentina and abroad. By those times the staff began to study the profiles exposed along rivers, creeks, roads and railways cuts in the area of Bahía Blanca in which Late Cenozoic sediments were represented. We joined the field work together with palynologists, sedimentologists and specialists in microinvertebrates that were already part of the team, with the aim of making our contribution from the point of view of vertebrate paleontology. The common idea was to make the reconstruction of the geological and paleoenvironmental evolution of the area.

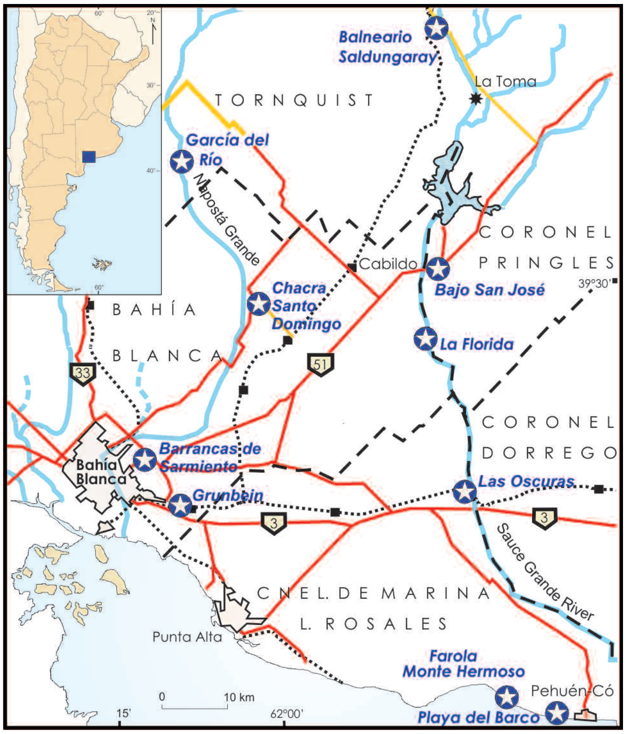

Figure 1. Location map showing the studied localities. Grünbein represents three quarries very close to each other: canteras Seminario, Vialidad and Relleno Sanitario.

During field work, several exposures appropriate for multidisciplinary study were found. In some of them the vertebrate record was scarce, but anyway they were significant when making the correlation with other localities. In this way, a wider span of time and geographic area could be studied.

The first results were limited to specific localities (*e.g.*, Quattrocchio *et al.*, 1988; Deschamps and Borromei, 1992; Deschamps and Tonni, 1992; Verzi and Deschamps, 1996; Deschamps *et al.*, 1998), but with time, data were used to make bio-chronostratigraphic proposals (Deschamps, 2003, 2005), which were refined in subsequent papers (*e.g.,* Verzi *et al.*, 2004a, 2008; Deschamps *et al.*, 2012, 2013; Tomassini, 2012; Tomassini and Montalvo, 2013; Tomassini *et al.*, 2013a) even making inferences about environmental conditions suggested by the recorded taxa. In this sense, rodents were particularly important among mammals (Verzi *et al.*, 2004a; Quattrocchio *et al.*, 2008; Deschamps *et al.*, 2009, 2012, 2013; Tomassini *et al.*, 2013a; Vucetich *et al.*, 2014a,b, 2015).

The purpose of the present contribution is to provide an update of both the stratigraphic proposal, and the mammal systematics on which it is based, for the Late Miocene–Holocene interval, within an area of the southwest of the Buenos Aires Province between 38° 20'–39° S, and 61° 35'–62° 10' W (Fig. 1). In this way, we wish to acknowledge Dr. Mirta Quattrocchio and to offer this work as a tribute for the influence she has had on the development of our careers.

GEOLOGICAL SETTING

The oldest sediments bearing vertebrate remains in this area correspond to the Late Miocene interval and form the regional substrate above which the present relief was elaborated (Zárate, 2005). These are massive to coarsely stratified, brownish red to yellowish sandy silts ending with a massive carbonate level, known as "Pampean sediments". The exposures are generally isolated along the banks of drainage systems. Different lithostratigraphic units were named for these sediments (some of them without the requirements of the stratigraphic Argentinean code CAE, 1992), *e.g.*, Arroyo Chasicó (Pascual, 1961), Epecuén (Pascual, 1961), Pampiano (Fidalgo *et al.*, 1973), La Norma (De Francesco, 1992), Irene (Reig, 1955), Saldungaray and La Toma (Furque, 1967) formations. Folguera and Zárate (2009, 2011) gathered them as the Cerro Azul Formation and interpreted that they represent distal sinorogenic facies that document the Andean tectonic dynamic. Folguera and Zárate (2009) and Montalvo *et al.* (2012) proposed an evolutionary, regional geological model to explain the geographical distribution and antiquity of the faunal emblages found in the Cerro Azul Formation (see Verzi, 1999). According to the fossil content it includes deposits of the Chasicoan and Huayquerian ages (Fig. 2). The accumulation of these sediments began after the regression of the Paranense sea, identified in northeastern Argentina as Paraná and Entre Ríos formations (*sensu* Chebli *et al.*, 1999), and Barranca Final Formation in northeastern Patagonia (Colorado Basin; Zambrano, 1972). The establishment of these diverse groups of environments that favored the development of continental vertebrates was called Edad de las Planicies Australes (the age of the austral plains) by Pascual and Bondesio (1982). According to Zárate (2005) there was a progressive trend towards cooling and aridization, with alternating wetter and warmer conditions. In most sections sedimentation was related to fluvial agents or water bodies; eolian facies were subordinated, although through time they became dominant.

Pliocene sediments were grouped together with those Late Miocene ones as the “Araucanense”. They include the Montehermosan and Chapadmalalan ages. Several exposures, mainly represented by cliffs located in the Atlantic coast, yielded abundant mammal remains, being the most significant those of Farola Monte Hermoso and the area of Mar del Plata-Miramar, which are mostly related to fluvial environments.

The sedimentary record of the latest Pliocene–Pleistocene is represented by fluvial and aeolian sequences which are subject of several stratigraphic proposals in different areas of the Buenos Aires Province (see Zárate, 2005). Landscape reactivation occurs with the development of valleys carved in the Mio–Pliocene substrate. The fluvial Late Pleistocene-Holocene units are the equivalents to the Luján Formation of northeastern Buenos Aires Province (Fidalgo *et al.*, 1973): Agua Blanca Formation (De Francesco, 1992, and modifications of Rabassa, 1989, and Zavala and Quattrocchio, 2001) or part of the San José Sequence and Agua Blanca Sequence (Zavala and Quattrocchio, 2001), as well as the Chacra La Blanqueada Formation (Rabassa, 1989), the youngest fluvial unit, corresponding to overflow sediments. The eolian sediments of this interval are included in the Saavedra Formation (De Francesco, 1992), equivalent to the La Postrera Formation of eastern Buenos Aires Province (Fidalgo *et al.*, 1973), and Matadero Saldungaray Formation (Rabassa, 1989), which represents the youngest eolian sediments of historical times.

Zavala and Quattrocchio (2001) produced a chronostratigraphic chart in which they proposed the relationships

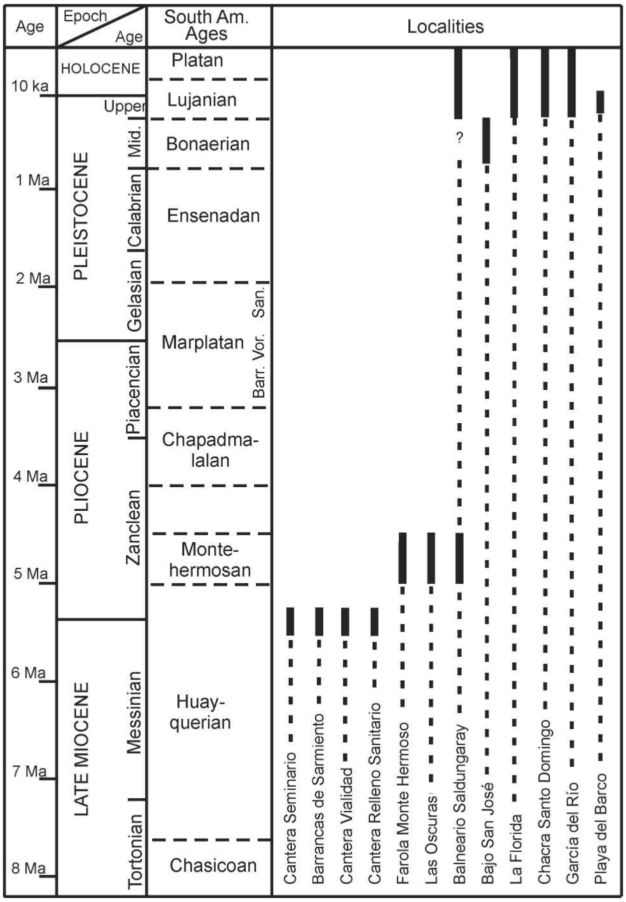

Figure 2. Stratigraphic chart showing the levels exposed at the studied localities correlated with International and South American ages.

among the lithostratigraphic units of the Late Cenozoic. The finding of mammals in many of them (Verzi *et al.*, 2004a, 2008; Deschamps, 2005; Tomassini *et al.*, 2010, 2013a; Deschamps *et al.*, 2012, 2013) together with numerical ages (*e.g.*, Aramayo, 1997; Schultz *et al.*, 2006) allowed improving their temporal assignment.

STUDIED LOCALITIES

The localities representing the Late Miocene–Holocene interval selected for this contribution will be listed according to the age of the exposed sediments from oldest to youngest. See complete list of taxa in Appendix 1.

Late Miocene–Pliocene

This interval was studied in quarries near Bahía Blanca and cliffs of the Sauce Grande River and the Atlantic coast.

1) Cantera Seminario

Location: 38° 44′ 08′′ S, 62° 12′ 19′′ W; 58–68 m height (see Grünbein in Figs. 1, 3.1).

Bearing unit: Cerro Azul Formation (*sensu* Folguera and Zárate, 2009). The section is 11 m thick and was divided into five levels. Fossils were found in the upper part of level 2, below the calcrete crust.

Biostratigraphic units recognized in the sequence: type section of the *Xenodontomys ellipticus* Zone (Verzi *et al.*, 2008).

Age: Late Huayquerian (Late Miocene–earliest Pliocene; late Messinian–early Zanclean; see below; Deschamps *et al.*, 2013).

Fossil content: the octodontid rodents *Xenodontomys ellipticus* and *Phtoramys* cf. *P. hidalguense* are important biostratigraphic indicators (see Deschamps *et al.*, 1998; Deschamps, 2005; Verzi *et al.*, 2008 for details). Other taxa include: *Doellotatus* cf. *D. inornatus*, *D.* cf. *D. praecursor*, *Chorobates* sp., *Paedotherium* cf. *P. minor*, *Tremacyllus* cf. *T. impressus*, *Orthomyctera* sp., cf. *Palaeocavia*) and *Lagostomus* sp. (we follow Rasia, 2016 for the validity of "*Lagostomopsis*") (Fig. 4).

2) Barrancas de Sarmiento

Location: 38° 42′ 05′′ S, 62° 15′ 51′′ W; 50 m height (Figs. 1, 3.2).

Bearing unit: Cerro Azul Formation (*sensu* Folguera and Zárate, 2009).

Biostratigraphic units recognized in the sequence: Xenodontomys ellipticus Zone (Verzi *et al.*, 2008).

Age: Late Huayquerian (Late Miocene–earliest Pliocene; late Messinian–early Zanclean; see below; Deschamps *et al.*, 2013).

Fossil content: Xenodontomys ellipticus is an important biostratigraphic indicator (see Verzi and Deschamps, 1996; Deschamps, 2005; Verzi *et al.*, 2008 for details). Other taxa: *Paedotherium bonaerense, Lagostomus* sp., ?*Palaeocavia*, and Eutatini indet. (Fig. 5)

3) Cantera Vialidad

Location: 38° 45′ 19.89′′ S, 62° 09′ 39.75′′ W; 51–64 m height (see Grünbein in Fig. 1, 3.3).

Bearing unit: Cerro Azul Formation (*sensu* Folguera and Zárate, 2009).

Biostratigraphic units recognized in the sequence: Xenodontomys ellipticus Zone (Verzi *et al.*, 2008).

Age: Late Huayquerian (Late Miocene–earliest Pliocene; late Messinian–early Zanclean; see below; Deschamps *et al.*, 2013). This deposit has a numerical dating of 5.28±0.04 Ma (Schultz *et al.*, 2006).

Fossil content: Xenodontomys ellipticus is an important biostratigraphic indicator which allows correlations with Barrancas de Sarmiento and Cantera Seminario. Remains of this rodent were found in the same level of the dating, and also in overlying levels (Deschamps *et al.*, 2013; Deschamps and Tomassini, personal observations). Other unpublished taxa include *Paedotherium* sp., and *Chorobates villosissimus*.

4) Cantera Relleno Sanitario

Location: 38° 46′ 24′′ S, 62° 09′ 25′′ W; 12–24 m height (see Grünbein in Figs. 1, 3.4.)

Bearing unit: Cerro Azul Formation (*sensu* Folguera and Zárate, 2009). This section has 8 m mean thickness divided into five levels on the basis of calcrete crusts and paleosoils. Materials were recovered from two levels at the middle of the exposure.

Biostratigraphic units recognized in the sequence: Xenodontomys ellipticus Zone (Verzi *et al.*, 2008) because of the presence of *Phtoramys* cf. *P. hidalguense*.

Age: Late Huayquerian (Late Miocene–earliest Pliocene; late Messinian–early Zanclean; see below; Deschamps *et al.*, 2013).

Fossil content: From the lower Level 1 (paleosoil): cf. *Borhyaenidium Phtoramys* cf. *P. hidalguense*, *Macrochorobates* sp., *Promacrauchenia* sp.; Level 2 (calcrete level overlying the paleosoil): *Chasicotatus* cf. *C. peiranoi*, *Chorobates villosissimus*, *Macroeuphractus* cf. *M. morenoi*, cf. *Aspidocalyptus*, cf. *Berthawyleria*, *Paedotherium* cf. *P. minor*, *Tremacyllus* cf. *T. impresus*, and *Promacrauchenia* sp. (Fig. 6).

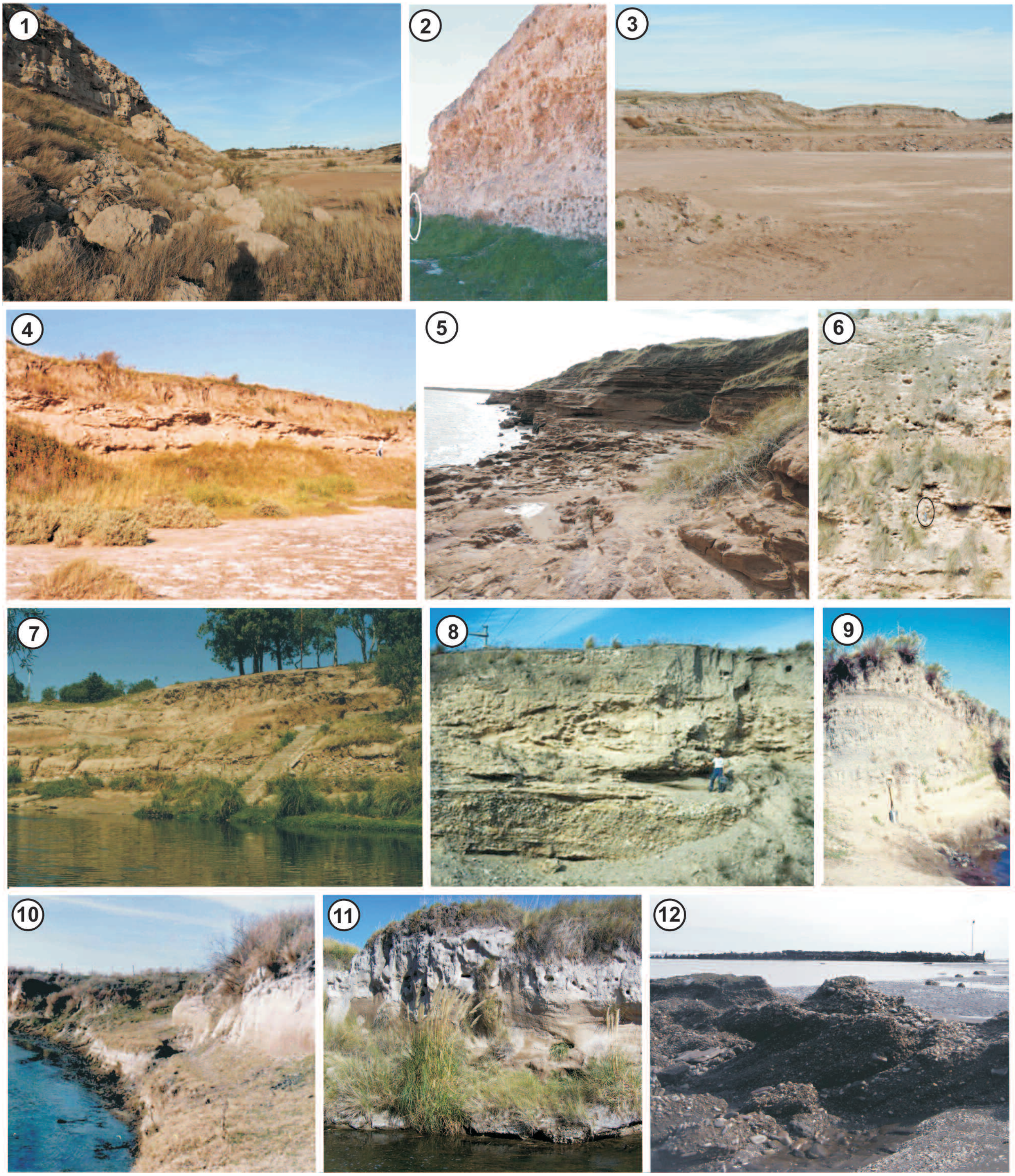

Figure 3. View of the exposures at the studied localities. **1,** Cantera Seminario; **2,** Barrancas de Sarmiento; **3,** Cantera Vialidad; **4,** Cantera Relleno Sanitario; **5,** Farola Monte Hermoso; **6,** Las Oscuras; **7,** Balneario Saldungaray; **8,** Bajo San José; **9,** Puesto La Florida; **10,** Chacra Santo Domingo; **11,** García del Río; **12,** Playa del Barco.

Figure 4. Mammals found in Cantera Seminario. **1,** osteoderm of ***Doellotatus*** cf. ***D. inornatus***; **2,** two osteoderms of ***Doellotatus*** cf. ***D. praecursor***; **3,** fragment of left mandible of ***Lagostomus*** sp.; **4,** fragment of right mandible of ***Phtoramys*** cf. ***P. hidalguense***; **5,** skull fragment of ***Orthomyctera*** sp.; **6,** skull and left mandible fragments of ***Xenodontomys ellipticus***. Anterior to the right (3,4) and to top (5,6). Scale= 1 cm (1, 2), 5 cm (3), 5 mm (4–6).

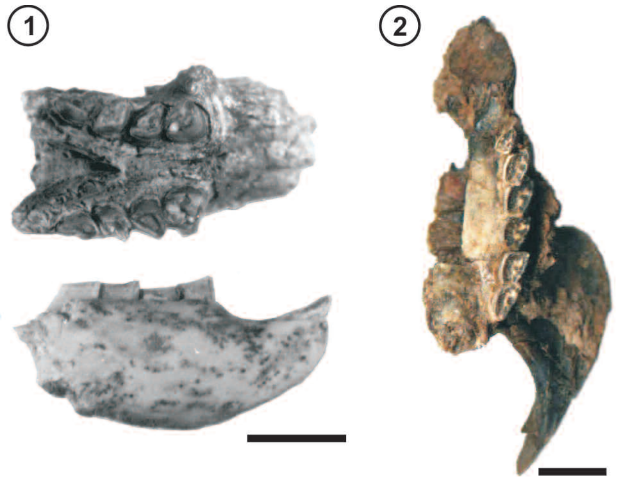

Figure 5. Mammals found in Barrancas de Sarmiento. **1,** skull fragment and right mandible of ***Xenodontomys ellipticus***; **2,** skull fragment of ***Paedotherium bonaerense***. Anterior to the right (1) and to top (2). Scales= 4 mm (1) and 1 cm (2).

5) Farola Monte Hermoso

Location: 38° 58′ 01′′ S, 61° 41′ 43′′ W; 0–10 m height (Figs. 1, 3.5).

Bearing unit: Monte Hermoso Formation (Zavala, 1993).

Biostratigraphic units recognized in the sequence: type section of the *Eumysops laeviplicatus* Range Zone (Tomassini *et al*., 2013a).

Age: Montehermosan (Early Pliocene; Zanclean; Tomassini *et al*., 2013a).

Fossil content: Eumysops laeviplicatus, Eumysops formosus, Eucelophorus cabrerai, Pithanotomys columnaris, Phugatherium cataclisticum are important biostratigraphic indicators (Deschamps *et al*., 2012, 2013; Tomassini *et al*., 2013a). Other frequent taxa include *Actenomys priscus*, *Paramyocastor diligens* (see Verzi *et al*., 2002), *Paedotherium bonaerense*, *Paedotherium typicum*, *Tremacyllus impressus*, *Doellotatus inornatus*, *Eoauchenia primitiva*, *Pseudotypotherium* sp. and *Plohophorus figuratus* (Fig. 7). See complete list in Appendix 1.

Recently, the knowledge of this fauna has been greatly increased with systematic, taphonomic, paleoenvironmental and paleobiogeographic contributions (*e.g.*, Zurita and Tomassini, 2006; Albino *et al*., 2009; Tomassini and Montalvo, 2010, 2013; Miño-Boilini *et al*., 2011; Tomassini *et al*., 2011, 2014a; Agnolin and Tomassini, 2012; Agnolin *et al*., 2014).

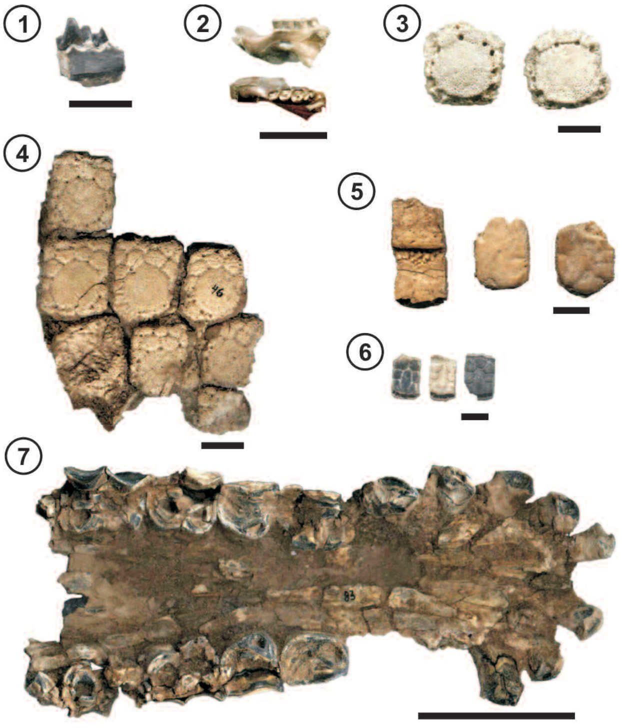

Figure 6. Some of the specimens found in Cantera Relleno Sanitario. **1,** mandible fragment of cf. ***Borhyaenidium***; **2,** mandible fragment of ***Phtoramys*** cf. ***P. hidalguense***; **3,** osteoderms of ***Aspidocalyptus*** sp.; **4,** carapace fragment of cf. ***Berthawyleria***; **5,** osteoderms of ***Macroeuphractus*** cf. ***M. morenoi***; **6,** osteoderms of ***Chasicotatus*** sp.; **7,** palate fragment of ***Promacrauchenia*** sp. Anterior to left (2) and to the right (7). Scales= 1 cm (1–6), 5 cm (7).

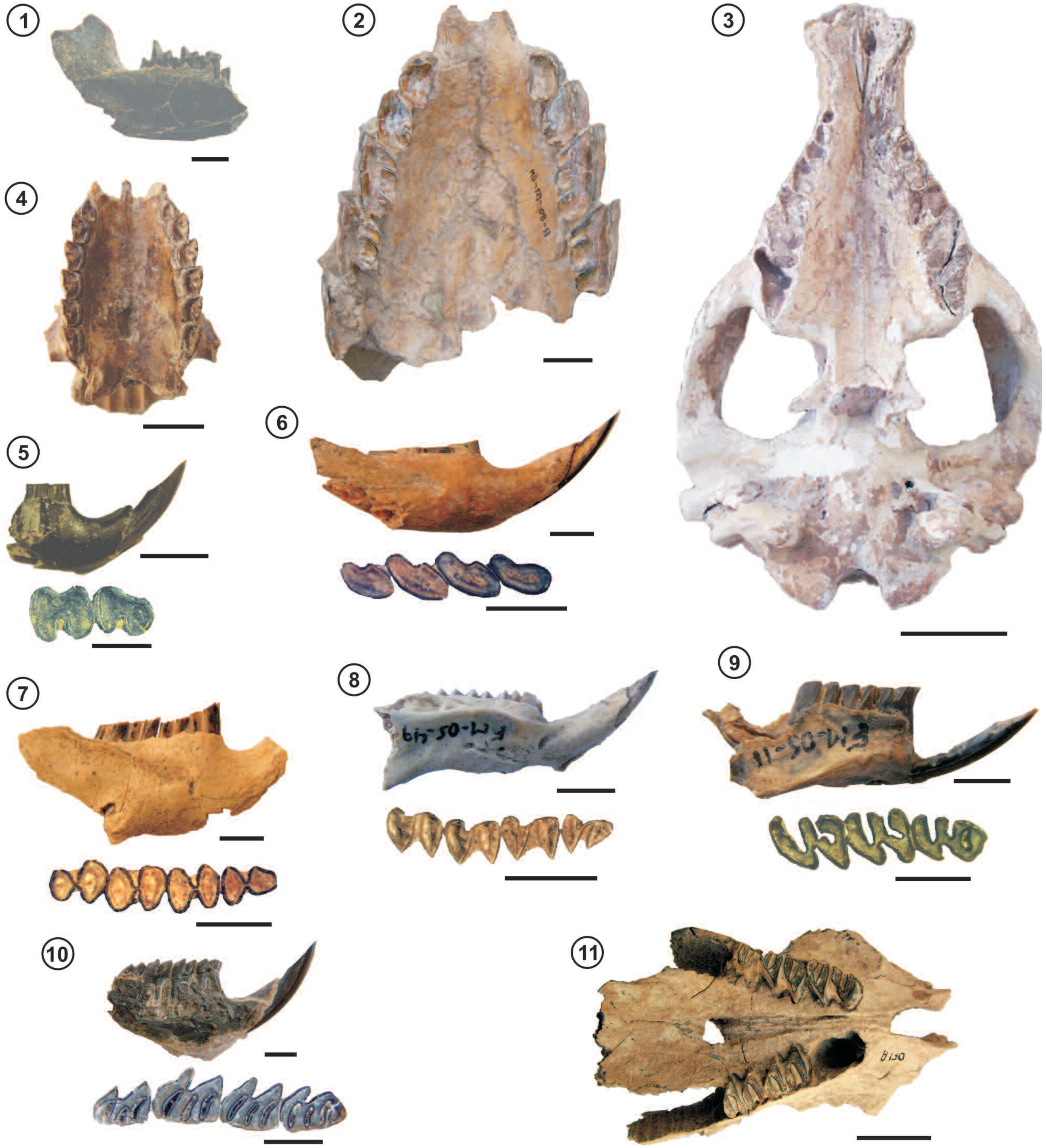

Figure 7. Some of the mammals found in Farola Monte Hermoso. **1,** left mandible fragment of ***Hyperdidelphys inexpectata*** (inverted); **2, skull fragment in ventral view of *Pseudotypotherium* sp.; 3, skull in ventral view of *Toxodon chapalmalensis*; 4, skull fragment in ventral view of *Paedotherium bonaerense*; 5–9,** right mandible fragments and detail of dental series in occlusal view of: **5, *Neophanomys*** sp.; **6, *Actenomys priscus*; 7, *Pithanotomys columnaris*; 8, *Palaeocavia*** sp.; **9, *Eumysops laeviplicatus*; 10,** left mandible fragment and detail of dental series in occlusal view (inverted) of ***Paramyocastor diligens*; 11,** skull fragment of ***Phugatherium cataclisticum***. Anterior to right (1, 5–11) and to top (2–4). Scales= 5 mm (A, E-J), 1 cm (B, D), 10 cm (C), and 2 cm (K).

According to Tomassini *et al.* (2013a) this biostratigraphic unit represents a brief lapse, included within a temporal range whose approximate boundaries are <5.28 Ma and 4.5/5.0 Ma.

6) Las Oscuras

Location: 38° 44′ 48.55′′ S, 61° 44′ 01.04′′ W; 82 m height (Fig. 1, 3.6).

Bearing unit: Saldungaray-La Toma formations (*sensu* Deschamps, 2005); Cerro Azul Formation (*sensu* Folguera and Zárate, 2009).

Biostratigraphic units recognized in the sequence: Actenomys priscus-Plohophorus cuneiformis Zone (Deschamps, 2005). This unit may correspond to the *Eumysops laeviplicatus* Range Zone defined in Farola Monte Hermoso (see discussion in Tomassini *et al.*, 2013a).

Age: Montehermosan (Early Pliocene; Zanclean; *sensu* Deschamps, 2005).

Fossil content: Actenomys priscus, *Plohophorus cuneiformis*, *Pseudotypotherium* sp., *Lagostomus* sp., *Orthomyctera* sp., *Dolicavia* sp., and *Epitherium laternarium* (Deschamps *et al.*, 1989; Deschamps, 2005).

The record of *Actenomys priscus*, with similar characteristics to the specimens recovered from Farola Monte Hermoso, plus the absence of the different species of *Xenodontomys*, support the proposed age.

Pleistocene–Holocene

This interval was studied in the banks of the Sauce Grande River and Napostá Grande Creek.

7) Sauce Grande River valley

a-Balneario Saldungaray

Location: 38° 11′ 52.30′′ S, 61° 46′ 11.39′′ W; 20 m height (Figs. 1, 3.7).

Bearing unit: The sequence begins with deposits of the Saldungaray Formation at the water level. This unit is overlain by coarse conglomerates and sands of the lower and upper sections of the San José Sequence (Zavala and Quattrocchio, 2001). Rabassa (1989) assigned these two latter units to the Agua Blanca Formation on the basis of two radiocarbon datings (32,300 +/- 1,800 RCYBP; Figini *et al.*, 1989; 27,500 +/- 670 RCYBP; Figini *et al.*, 1989; Rabassa, 1989) but geomorphology and stratigraphic position suggest an older age for these units. The profile ends with eolian deposits of the Matadero Saldungaray Formation.

Biostratigraphic units recognized in the sequence: The recorded taxa were insufficient to recognize any unit.

Age: Pliocene *s.l.* (Saldungaray Formation), Middle Pleistocene (San José Sequence according to Zavala and Quattrocchio, 2001 and Deschamps, 2005), or Late Pleistocene Agua Blanca Formation (according to Rabassa, 1989), Historical times–Present (Matadero Saldungaray Formation).

Fossil content: Mammal remains were very scarce. Saldungaray Formation: *Paedotherium bonaerense*; San José Sequence, lower section: *Glossotherium* sp. and *Lama* sp.; upper section *Lagostomus* sp.; Matadero Saldungaray Formation: *Ctenomys talarum* and *Lepus europaeus*.

b-Bajo San José

Location: 38° 29′ 12.10′′ S, 61° 46′ 59.60′′ W; 125 m height (Figs. 1, 3.8).

Bearing unit: San José Sequence (Zavala and Quattrocchio, 2001), especially a sandy lens up to 1 m thick of the lower section that yielded most of the small vertebrates, 2 m from the base of the profile.

Biostratigraphic units recognized in the sequence: type section of the *Ctenomys kraglievichi* Zone (Verzi *et al.*, 2004a). The zone was also recognized at Las Grutas-Punta Negra in Necochea (southeastern Buenos Aires Province), as well as in Camet and Constitución, in the cliffs north of Mar del Plata.

Age: Bonaerian (Middle Pleistocene; Verzi *et al.*, 2004a)

Fossil content: the ctenomyid rodent *Ctenomys kraglievichi* as well as the dasypodid *Tolypeutes* sp. nov. (Scillato-Yané in Deschamps, 2005) are important biostratigraphic indicators, exclusive of the Bonaerian. Other taxa include: Pisces (*Pimelodella* aff. *P. laticeps*, *Callichthys callichthys*, *Percichthys* sp., *Corydoras* cf. *C. paleatus*), turtles (*Hydromedusa tectifera*), birds (*Rhea* sp., *Chloephaga* sp. 1, *Chloephaga* sp. 2, *Porphyrio* sp., cf. *Pseudoseisura cursor-Pseudoseisuropsis nehuen*, Motacillinae indet.), marsupials (*Lestodelphys* sp.), dasypodids (*Chaetophractus villosus*, *Zaedyus pichiy*, *Eutatus seguini*, *Propraopus* sp.), glyptodontids (*Glyptodon clavipes*, *Doedicurus* sp., *Panochthus tuberculatus*, *Sclerocalyptus* cf. *S. ornatus*), sloths (*Scelidotherium* cf. *S. leptocephalum*, *Glossotherium* sp., *Lestodon armatus*, *Megatherium americanum*), litopterns (?*Macraucheniopsis ensenadensis*), notoungulates (*Toxodon* sp.), cricetid rodents (*Akodon* cf. *A. azarae*, *Akodon* cf. *A. inisca-*

tus, *Oxymycterus* sp., *Reithrodon auritus*, *Phyllotis* sp., *Lundomys* sp.), caviomorph rodents (*Microcavia* sp., *Galea* sp., *Lagostomus* sp., *Neochoerus* cf. *N. tarijensis*, *Myocastor columnaris*), Gomphotheriidae indet., artiodactyls (Tayassuinae indet., *Lama* sp., Cervidae indet.), perissodactyls (*Hippidion principale*), and carnivores (*Pseudalopex* sp., cf. *Herpailurus*) (Fig. 8). See complete list in Appendix 1.

The oldest records of *Callichthys callichthys*, *Percichthys*, *Porphyrio*, *Herpailurus*, *Lundomys*, *Oxymycterus*, *Phyllotis*, and Tayassuinae (Cione and López Arbarello, 1995; Pardiñas and Deschamps, 1996; Prevosti, 2006; Pardiñas and Teta, 2011; Gasparini, 2013) come from this site.

Some taxa are significant from a biogeographic point of view. Among Osteichthyes, the pimelodid siluriformes *Pimelodella*, *Callichthys* and *Corydoras*, and the Percichthydae *Percichthys* are not simpatric today. The southern border of the geographic distribution of *Callichthys* is currently farther north within the Buenos Aires Province, and on the contrary, *Percichthys* inhabits today the Austral Subregion (Cione and López Arbarello, 1995). This is the southernmost record of the turtle *Hydromedusa tectifera* which today inhabits the Neotropical Region up to northern Argentina (de la Fuente, 1992, 1999).

As well, other taxa are important in view of their paleoenvironmental meaning (for details see Pardiñas and Deschamps, 1996; Deschamps, 1998; Deschamps *et al.*, 2000; Verzi *et al.*, 2004a; Deschamps, 2005; Prevosti, 2006; Pardiñas and Teta, 2011; Gasparini, 2013).

The birds record is outstanding because three orders are represented, Anseriformes, Gruiformes and Passeriformes (Tonni and Deschamps, 2001). Anseriformes, Family Anatidae, include several remains of small indeterminate anatids and *Chloephaga*. This genus would be represented by two new species. Gruiformes is represented by the Family Rallidae, genus *Porphyrio*. Passeriformes are recorded by a large furnariid similar to *Pseudoseisura cursor* and *Pseudoseisuropsis nehuen* (both from the Ensenadan of the Buenos Aires Province; Tonni and Noriega, 2001) and an indeterminate passeriid of the Family Motacillinae. Modern *Pseudoseisura* are widely distributed in South America inhabiting arid environments, but both species of *Porphyrio* inhabit intertropical South America. This means that *Porphyrio* would join *Callichthys*, *Hydromedusa* and *Lundomys* in warm and humid environments, and *Chloephaga* would join *Percichthys*, *Lestodelphys*, *Phyllotis* and *Akodon iniscatus* among the taxa adapted to more arid and/or colder environments.

c-Puesto La Florida

Location: 38° 35′ S, 61° 45′ W; 108 m height. This site is located at the Sauce Grande River valley between Bajo San José and Las Oscuras localities (Fig. 1, 3.9).

Bearing unit: middle and upper sections of the Agua Blanca Sequence, Chacra La Blanqueada and Matadero Saldungaray formations (Zavala and Quattrocchio, 2001).

Biostratigraphic units recognized in the sequence: type section of the *Ozotoceros bezoarticus* Zone in the upper section of the Agua Blanca Sequence, and *Bos taurus-Ovis aries* Zone in upper levels of the Chacra La Blanqueada and Matadero Saldungaray formations (Deschamps, 2005).

Age: Lujanian (Late Pleistocene–Early Holocene) for the Middle Section of the Agua Blanca Sequence; Platan (Late Holocene) for the Upper Section of the Agua Blanca Sequence; Platan (Late Holocene)–Present for the Chacra La Blanqueada Formation at this site; historical times–present for the Matadero Saldungaray Formation (Deschamps, 2005). In the cliffs of the Sauce Grande River near Bajo San José, Borromei (1995) reported radiocarbon datings for the upper section of the Agua Blanca Sequence (5010±120 years ^{14}C BP) and Chacra la Blanqueada Formation (2830±90 years ^{14}C BP) which restrict the age to the Middle and Late Holocene respectively. The Chacra La Blanqueada Formation was also dated on peat wood samples between 1570 ± 70 and 900±50 years ^{14}C BP at La Toma locality (Rabassa, 1989; Rabassa *et al.*, 1991).

Fossil content: Middle section of the Agua Blanca Sequence: *Lama guanicoe.* Upper section of the Agua Blanca Sequence: *Rhea americana*, cf. *Anas*, *Chaetophractus villosus*, *Zaedyus pichiy*, *Cavia aperea*, and *Ozotoceros bezoarticus*. Chacra La Blanqueada and Matadero Saldungaray formations: *Bos taurus*.

8) Napostá Grande Creek valley

a-Chacra Santo Domingo

Location: 38° 33′ 45.14′′ S, 62° 04′ 17.27′′ W; 98 m height. This site is in the middle valley of the Napostá Grande Creek; access from Bahía Blanca City is through the road known as La Carrindanga (Figs. 1, 3.10).

Bearing unit: middle and upper sections of the Agua Blanca

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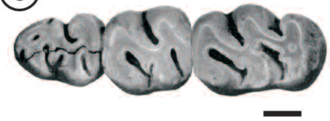

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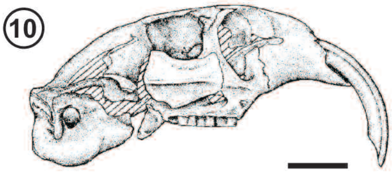

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Sequence, Chacra La Blanqueada and Matadero Saldungaray formations (Zavala and Quattrocchio, 2001).

Biostratigraphic units recognized in the sequence: type section of the *Equus* (*Amerhippus*) *neogaeus-Macrauchenia patachonica* Zone, in the middle section of the Agua Blanca Sequence (Deschamps, 2005), and type section of the *Bos taurus-Ovis aries* Zone in the Matadero Saldungaray Formation.

Age: Lujanian (Late Pleistocene–Early Holocene) for the Middle Section of the Agua Blanca Sequence; Platan (Late Holocene) for the Upper Section of the Agua Blanca Sequence (this unit yielded neospecies and a radiocarbon dating of 1960±100 ^{14}C years BP; see Deschamps and Tonni, 1992); Platan (Late Holocene) for the Chacra La Blanqueada Formation at this site; historical times for the Matadero Saldungaray Formation (Deschamps, 2005).

Fossil content: Middle Section of the Agua Blanca Sequence: scarce remains of Rheidae indet., *Chaetophractus villosus*, *Scelidotherium leptocephalum*, *Macrauchenia patachonica*, *Lama guanicoe*, Lamini indet., and *Equus* (*A.*) *neogaeus*. The Upper Section yielded abundant remains, especially the lower levels: Cyprinodontiformes indet., Anura indet., *Rhea* sp., *Nothura darwini*, Tinamidae indet., *Anas* cf. *A. platalea*, *Dendrocygna* sp., and Anatidae indet., *Lestodelphys halli*, *Thylamys* cf. *T. pusillus*, *Chaetophractus villosus*, *Zaedyus pichiy*, *Holochilus brasiliensis*, *Calomys* cf. *C. laucha-musculinus*, *Reithrodon auritus*, *Ctenomys* sp., *Cavia aperea*, *Lama guanicoe*, *Ozotoceros bezoarticus*, and *Pseudalopex* aff. *P. gymnocercus*). Chacra La Blanqueada Formation: *Ctenomys talarum* and *Lama guanicoe*. Matadero Saldungaray Formation: *Lama guanicoe* and *Bos taurus* (Fig. 9).

b-García del Río

Location: 38° 21′ 49.70′′ S, 62° 09′ 05.32′′ W, 184 m height. Upstream of Napostá Grande village in the Napostá Grande Creek (Figs. 1, 3.11).

Bearing units: Middle and upper sections of the Agua Blanca Sequence, Chacra La Blanqueada and Matadero Saldungaray formations (Zavala and Quattrocchio, 2001).

Biostratigraphic units recognized in the sequence: the recorded taxa were insufficient to recognize any unit.

Age: the Upper Section of the Agua Blanca Sequence has a radiocarbon dating of 2610±60 years ^{14}C BP (Quattrocchio *et al.*, 1998), Late Holocene. Chacra La Blanqueada has a radiocarbon dating in this locality of 2342±47 years ^{14}C BP (Tomassini *et al.*, 2014b), Late Holocene.

Fossil content: Lama guanicoe was recorded in all units (Deschamps, 2005). Also, in Chacra La Blanqueada Formation *Ctenomys* cf. *C. talarum*, *Cavia aperea*, and *Chaetophractus villosus* were recovered (Tomassini *et al.*, 2014b).

10) Playa del Barco

Location: 39° 00′ 09′′ S, 61° 34′ 52′′W; 0–2 m height (Figs. 1, 3.12).

Bearing unit: San José Sequence (Zavala and Quattrocchio, 2001).

Biostratigraphic units recognized in the sequence: Equus (*Amerhippus*) *neogeus-Macrauchenia patachonica* Zone (Deschamps, 2005).

Age: Lujanian (Late Pleistocene–Early Holocene). A radiocarbonic dating yielded an age of 16.440±320 ^{14}C years BF (Aramayo, 1997). Some levels could include Bonaerian (Middle Pleistocene) fauna (see Zavala and Quattrocchio, 2001; Tomassini *et al.*, 2010).

Fossil content: Equus (*Amerhippus*) *neogeus*, *Macrauchenia patachonica*, *Glyptodon reticulatus*, *Doedicurus clavicaudatus*,

Figure 8. Some of the specimens found in Bajo San José. **1–7,** Aves. **1,** tarsus-metatarsus of ***Rhea*** sp.; **2–3,** ***Chloephaga*** sp. 1; **2,** left femur; **3,** left tarsus-metatarsus; **4–5,** ***Chloephaga*** sp. 2; **4,** right humerus; **5,** proximal fragment of left humerus; **6,** right humerus of Motacillinae indet.; **7,** left coracoid of cf. ***Pseudoseisura-Pseudoseisuropsis***; **8–13,** Rodentia. **8,** upper molars of ***Lundomys*** sp.; **9,** right mandible (inverted) of ***Akodon*** cf. ***A. iniscatus***; **10,** skull of ***Ctenomys kraglievichi***; **11,** palate fragment of ***Myocastor columnaris***; **12,** right mandible of ***Lagostomus*** sp.; **13,** skull of ***Neochoerus*** cf. ***N. tarijensis***; **14–15,** mandibles of Carnivora. **14,** ***Pseudalopex*** sp.; **15,** cf. ***Herpailurus***; **16–20,** Edentata. **16,** carapace fragment of ***Glyptodon clavipes***; **17,** osteoderm of ***Tolypeutes*** sp. nov.; **18,** osteoderm of ***Eutatus seguini***; **19,** osteoderm of ***Zaedyus pichiy***; **20,** right mandible fragment of ***Megatherium americanum***; **21,** left posterior autopodium of ?***Macraucheniopsis ensenadensis***; **22,** 3rd left lower incisor fragment of ***Toxodon*** sp.; **23,** molariforms of ***Hippidion principale***; **24,** mandible fragment with incisor of Tayassuinae indet.; **25,** molar of Gomphotheriidae indet. Anterior to the right (8–10, 12–15, 24), to top (11), and to the left (20). Scale= 1 cm (2–7, 10–12, 14–15, 17–19), 1 mm (8), 5 mm (9), 5 cm (1, 13, 21–23), 10 cm (16, 25).

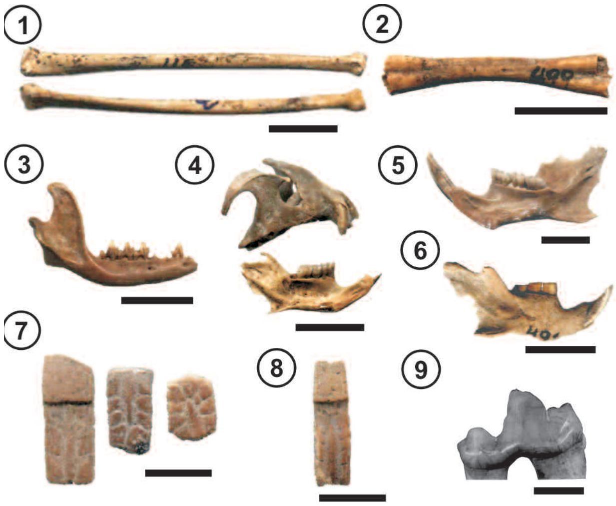

Figure 9. Some of the specimens found in Chacra Santo Domingo, Napostá Grande Creek. **1,** Aves, right humerus of ***Anas*** cf. ***A. platalea***; **2,** tibia-fibula of Bufonidae indet.; **3,** left mandible of ***Lestodelphys halli***; **4,** fragments of skull and mandible of ***Reithrodon auritus***; **5,** right mandible of ***Holochilus brasiliensis*** (inverted); **6,** mandible of ***Ctenomys*** sp.; **7,** osteoderms of ***Chaetophractus villosus***; **8,** osteoderm of ***Zaedyus pichiy***; **9,** p4 of ***Pseudalopex*** aff. ***P. gymnocercus.*** Anterior to the right (3–4, 6) and to the left (5). Scales= 1 cm (1–8) and 5 mm (9).

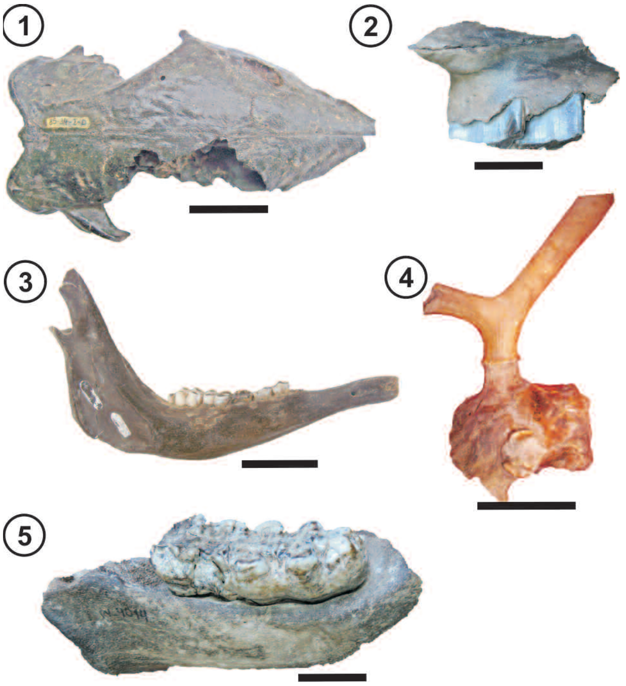

Figure 10. Some of the specimens found in Playa del Barco. **1,** skull of ***Eutatus seguini***; **2,** fragment of right maxilla of ***Toxodon platensis***; **3,** left hemimandible of Cervidae indet.; **4,** fragment of skull of ***Morenelaphus*** sp.; **5,** fragment of right hemimandible of ***Notiomastodon*** sp. Anterior to the right. Scales= 5 cm (1–3), 10 cm (4–5).

Eutatus seguini, *Scelidotherium leptocephalum*, *Lestodon armatus*, *Toxodon platensis*, *Notiomastodon platensis*, *Morenelaphus bonaerense*, *Hippidion* sp., *Smilodon populator*, *Neochoerus* cf. *N. tarijensis*, among others (Fig. 10; see complete list in Appendix 1).

SYSTEMATIC, BIOCHRONOSTRATIGRAPHIC AND PALEOENVIRONMENTAL COMMENTS

As mentioned above, since the idea of Mirta Quattrocchio of facing multidisciplinary studies, paleontologic survey in southwestern Buenos Aires Province was increased, and is still increasing today. This was reflected directly in enlarged collections which in turn allowed improving the knowledge of the vertebrate communities that inhabited the area during the last 10 My. In this context, those localities in which units formed by fluvial deposits are exposed (*e.g.*, Farola Monte Hermoso, Bajo San José, Playa del Barco), yielded the largest amounts and diversity of bone remains. Together with pollen and ostracodes analyses, vertebrate taxa helped inferring paleoenvironmental, paleoclimatic and paleobiogeographic conditions both in the Mio–Pliocene and Quaternary.

The age of the late Cenozoic continental deposits and the included fauna is a major issue. Given the scarcity of numerical dating, the age has been almost always determined on the basis of fossil distribution, which makes boundaries and temporal extension of biostratigraphic units at least uncertain and controversial (see Cione and Tonni, 1995, 2005; Verzi *et al.*, 2008; Deschamps *et al.*, 2013). Multidisciplinary studies accomplished in the last years, including detailed fieldwork, paleontological prospection with precise data of stratigraphic provenance, systematics, sedimentological analyses, sequential stratigraphy, taphonomy, magnetostratigraphy, among others, resulted in an improvement of biochronostratigraphic schemes.

One of the main advances in this regard is the inference of the age of “Huayquerian” and “Montehermosan” faunas. Among mammal faunas, rodents are very useful as biostratigraphic tools because of their wide geographic distribution, and high reproductive and rapid evolutionary rates (Vianey-Liaud *et al.*, 2011). The knowledge of the systematics and phylogeny of several groups of rodents recorded in these intervals has been largely improved in recent years (*e.g.*, Octodontidae, Ctenomyidae, Echimyidae, Hydrochoeridae). This turned out to be quite significant because many of them are good biostratigraphic indicators (Vucetich *et al.*, 2005; Verzi, 2008 and literature therein; Olivares 2009; Olivares *et al.*, 2012; Deschamps *et al.*, 2013 and literature therein).

In the study area, "Huayquerian" faunas were found in Cantera Seminario, Cantera Relleno Sanitario, Cantera Vialidad, and Barrancas de Sarmiento. These localities have in common the record of *Xenodontomys ellipticus* which is an octodontid rodent that pertains to the *Chasichimys-Xenodontomys* lineage. The polarity shown by their anagenetic evolutionary pattern led Verzi *et al.* (2004b) to propose that *X. ellipticus* is younger than *X. simpsoni* (from Los Salitrales Formation, Buenos Aires Province, and several localities of the Cerro Azul Formation in La Pampa Province) and older than *X. elongatus* (found in the Cerro Azul Formation cropping out at Caleufú, La Pampa Province). It is noteworthy that two other lineages of octodontid rodents (*Neophanomys* and *Reigechimys*; Verzi *et al.*, 2011; Sostillo *et al.*, 2014) support the scheme based on the lineage of *Xenodontomys*. The trend toward increasing hypsodonty observed in the lineage of *Xenodontomys* and in other caviomorph rodents is related to adaptations to open environments within the climatic deterioration of the Late Miocene (Verzi, 2001). Given that Cantera Vialidad yielded remains of *Xenodontomys ellipticus* in the same levels and above those which have a numerical dating of 5.28±0.04 Ma (Schultz *et al.*, 2006) it may be concluded that "Huayquerian" faunas in this area are latest Miocene–earliest Pliocene in age.

On the other hand, "Montehermosan" faunas were found in Farola Monte Hermoso and Las Oscuras. Deposits of the Monte Hermoso Formation in its type locality Farola Monte Hermoso were accumulated in a dynamic fluvial environment of high-sinuosity rivers ("muddy fine-grained rivers" in Miall, 1985). In these localities, none of the species of *Xenodontomys* has been recorded, being instead abundant *Actenomys priscus*, the most derived representative of the lineage *Xenodontomys–Actenomys* (Verzi, 2008). In addition, when these specimens are compared to specimens of *A. priscus* found in levels assigned to the Chapadmalalan (from the area of Mar del Plata-Miramar), the latter display a more derived dental morphology (Deschamps, 2003; Tomassini *et al.*, 2013a). Preliminary observations (Tomassini, 2012) showed that the specimens of *Neophanomys* found in Farola Monte Hermoso are also more derived than the species recognized for the Huayquerian Stage/Age of La Pampa (*N. pristinus* and *N. recens*), Catamarca (*N. biplicatus*) and Mendoza (*N. biplicatus*). Hence the Montehermosan assemblages cannot be older than Early Pliocene because the evolutionary stage of these octodontids (and also other groups of mammals; see Tomassini, 2012; Deschamps *et al.*, 2012; Tomassini *et al*, 2013a) supports the idea that the bearing sediments of the Monte Hermoso Formation are younger than those of the Cerro Azul Formation at Caleufú with "Huayquerian" fauna.

Another group of rodents found in the area that turned out to be very indicative from a biochronologic point of view are the giant capybaras. The study of the dental evolution of this family resulted in a new interpretation of their taxonomy and systematics which involved the ontogenetic change (Vucetich *et al.*, 2005, 2014a,b, 2015; Deschamps *et al.*, 2007, 2009, 2013). Currently, a single taxon is recognized for each level, and although they were not found in a single stratigraphic sequence to test the proposal, the accompanying fauna supports the different age inferred for each taxon. In "Huayquerian" assemblages only the genus *Cardiatherium*, with different species, is recorded (Vucetich *et al.*, 2005; 2014b). Instead in "Montehermosan" and "Chapadmalalan" assemblages, *Phugatherium* is recorded, with two species in the study area, *P. cataclisticum* in Farola Monte Hermoso and *P. novum* in the area of Mar del Plata-Miramar (Deschamps *et al.*, 2012, 2013). Capybaras were one of the keys to suggest that a single biostratigraphic unit could be determined in the Monte Hermoso Formation at Farola Monte Hermoso, different form the one recognized in the area of Mar del Plata-Miramar. This is supported by other rodent lineages such as the different species of the echimyid rodent *Eumysops* (Olivares *et al.*, 2012) found in these localities (Deschamps *et al.*, 2012; Tomassini *et al.*, 2013a).

Concerning the age of the assemblages, the determination of the extension and the boundaries of the represented Stage/Age or SALMA has been long debated, especially those between Huayquerian and Montehermosan. A common use is to extend the boundaries of the different biostratigraphic units represented in a certain interval in order to obtain a continuous sequence, even without numerical dating or faunistic record that support these interpretations. In recent years, taphonomic and sedimentological studies carried out in several localities of the Pampean Region suggested that most assemblages actually represent a very short interval (*e.g.*, Arroyo Chasicó, Laguna Chillhué, Caleufú, Farola Monte Hermoso among others; Tomassini and Montalvo, 2013; Tomassini *et al.*, 2013a,b). We suggest restricting the assemblage duration to the represented interval, considering the existence of hiatuses between the following or previous assemblages instead of extending the duration up to the contiguous unit. In this sense, the assemblages would be like temporal windows in the stratigraphic column, which only show the moment of the assemblage, being the rest hidden. Their relative chronology, and partly the extension of the hiatuses between each other are given by the interpretation of taxonomic differences derived from the processes of anagenesis, extinction and migration (Montalvo *et al.*, 2012; Tomassini *et al.*, 2013b). This idea was somehow implicit when the non-contemporaneity of some "Huayquerian" assemblages was proposed (*e.g.*, Verzi *et al.*, 2008; Deschamps *et al.*, 2013).

Taking a look at the time represented in the studied localities according to the mammal record (see Fig. 2), it is evident that the interval between the Montehermosan and Bonaerian (Chapadmalalan, Marplatan and Ensenadan, or following our scheme, the Late Pliocene–Early Pleistocene) is not represented in the area or has not been found yet. During this interval, even the sedimentological record is poor, because this area would have been affected by erosion processes and no deposition (Quattrocchio *et al.*, 2008). Certainly the regional geological model proposed to explain the geographical distribution and antiquity of the faunal associations will help in elucidating this issue.

The Bonaerian is represented at Bajo San José. The deposits of the San José Sequence in this locality were accumulated by a braided river (Borromei, 1990). The age of the locality was inferred through the record of *Ctenomys kraglievichi*. This large and peculiar octodontid rodent was also found in Pleistocene localities of the Atlantic coast (Necochea, northern Mar del Plata, and also Uruguay; Verzi *et al.*, 2004a). No absolute dating is known so far for the levels bearing *Ctenomys kraglievichi*, but biochronological and paleomagnetic data suggest a relative dating of this unit. Among the first ones, the association with *Tolypeutes* sp. nov. and *Hippidion principale*, together with *Megatherium americanum*, *Glyptodon clavipes* and *Panochthus tuberculatus*, whose biochrons encompass the Bonaerian–Lujanian. Regarding paleomagnetic data, *Ctenomys kraglievichi* is recorded at least 2.2 m above the Bruhnes-Matuyama magnetostratigraphic boundary in northern Mar del Plata, which suggests a younger age than 0.78 Ma.

With respect to the paleoclimatic inferences, *C. kraglievichi* is associated in Bajo San José and the other localities, with other caviomorph rodents that represent an immigration event triggered by an important warm climatic pulse (Vucetich *et al.*, 1997; Vucetich and Verzi, 2002). The finding of the specimens of Necochea was quite significant. This rodent appears in a single sequence with other micromammal remains. The extinction of the taxa found in older levels is accompanied by the sudden appearance of *C. kraglievichi* associated with the single record of a post-Pliocene eumysopine echimyid rodent at this latitude, and the single dasyproctid recorded in the Pleistocene of Argentina. Both species and *C. kraglievichi* are clearly Brazilian immigrants to the southern-southeastern Buenos Aires Province. In Bajo San José, *C. kraglievichi* is associated with sigmodontine rodents (*e.g.*, *Lundomys*; Pardiñas and Deschamps, 1996) and a tayassuine also suggesting a strong warm pulse. This warm pulse is in agreement with the relative high sea level proposed for the deposition of the San José Sequence through the analysis of sequence stratigraphy (Zavala and Quattrocchio, 2001). The climatic change identified in the *C. kraglievichi* Zone may correspond to the warm pulse at 0.4 Ma of the MIS 11 (see discussion in Verzi *et al.*, 2004a).

Mammal remains from the Late Pleistocene in the area are scarce, but suggest that it was a mostly arid period. After the influence of immigrant mammals entering through the Panamá corridor from Central and North America in the set of events known as GABI (Great American Biotic Interchange), the composition of the mammal assemblages was already established. The major changes observed since the extinction of the megafauna are mostly due to responses to climatic-environmental change. The reaction is more evident in those populations that inhabit the extremes of the geographical distribution of the species (Millien *et al.*, 2006, and literature therein). Precisely, the southwest of the Buenos Aires Province is an ecotonal area between the Guayano-Brasileña and Andino-Patagónica Subregions (*sensu* Ringuelet, 1961), where the extremes of the geographical distribution of the species from both subregions are in close interaction.

This interval is recorded in Puesto La Florida, Chacra La Blanqueada, García del Río, Balneario Saldungaray, and Playa del Barco. The deposits are similar to those found in the banks of rivers and creeks of the east of the Buenos Aires Province (the Pampa Ondulada and Interserrana) with Lujanian deposits. They correspond mainly to channel deposits of plains rivers with differences related to the proximity of the ranges.

Holocene deposits are recorded in the same localities, overlying the Late Pleistocene levels. They are also similar to those of the Pampa Ondulada and Interserrana where the Platan was recognized. Most of the remains were found in the upper levels of the middle section of the Agua Blanca Sequence. In this sector of the profile, a conspicuous lamination is observed. The best represented locality of this interval is Chacra Santo Domingo, where a Brazilian and/or aquatic vertebrate fauna (fish, anurans, *Anas platalea*, *Dendrocygna*, *Holochilus brasiliensis* and *Cavia aperea*) agree with the hydrophytic communities found in pollen analyses. The southern expansion of Brazilian fauna coexisted with central and Patagonian elements (*Chaetophractus villosus*, *Zaedyus pichiy*, *Lama guanicoe*, *Reithrodon auritus*, *Pseudalopex gymnocercus*, among others) suggesting the amelioration of previous arid and semiarid conditions. As well, water bodies could have locally modified the arid conditions favoring the ingression of the Brazilian fauna, and the presence of endemic forms could have been favored by the influence of the nearby ranges (Quattrocchio *et al.*, 1988; Deschamps and Tonni, 1992).

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APPENDIX 1. Systematic list. Record in the studied localities.

Taxa	*Localities*											
	CS	*BSar*	*CV*	*CRS*	*FMH*	*LO*	*BalS*	*BSJ*	*PLF*	*CSD*	*GdR*	*PdB*
Class Osteichthyes												
Order Siluriformes												
Pimelodella *aff.* **P. laticeps** *Eigenmann, 1917*								*X*				
Callichthys callichtys *Linné, 1758*								*X*				
Corydoras *cf.* **C. paleatus** *(Jenyns, 1842)*								*X*				
Siluriformes indet.					*X*							
Trichomycteridae indet.					*X*							
Order Perciformes												
Percichthys *sp.*								*X*				
Plesiopercichthys dimartinoi *Agnolin et al., 2014*					*X*							
Order Characiformes												
Characidae indet.					*X*							
Class Amphibia												
Order Anura												
Rhinella *cf.* **R. pisanoi** *Casamiquela, 1967*					*X*							
Rhinella *cf.* **R. schneideri** *Werner, 1894*					*X*							
Ceratophrys ameghinorum *Fernicola, 2001*					*X*							
Lepidobatrachus australis *Nicoli, 2015*					*X*							
Leptodactylus *sp.*					*X*							
Class Reptilia												
Order Chelonii												
Chelonoidis australis *(Moreno, 1889)*					*X*							
Hydromedusa tectifera *(Cope, 1869)*								*X*				
Order Squamata												
Tupinambis *sp.*					*X*							
Callopistes bicuspidatus *Chani, 1976*					*X*							
Colubridae indet.					*X*							
aff. **Bothrops** *Wagler, 1824*					*X*							
Boa *sp.*					*X*							
Class Aves												
Order Anseriformes												
Anas platalea *Vieillot, 1816*								*X*		*X*		
Anas *sp.*									*X*			
Chloephaga *sp. 1*								*X*				
Chloephaga *sp. 2*								*X*				
Dendrocygna *sp.*										*X*		
Dendrocygninae indet.					*X*							
Anatidae indet.										*X*		
Order Tinamiformes												

Taxa	*Localities*											
	CS	*BSar*	*CV*	*CRS*	*FMH*	*LO*	*BalS*	*BSJ*	*PLF*	*CSD*	*GdR*	*PdB*
Nothura parvula *Tambussi, 1989*					*X*							
Nothura darwini *Gray, 1840*								*X*		*X*		
Eudromia *cf.* **E. elegans** *Geoffroy St. Hillaire, 1832*					*X*							
Eudromia olsoni *Tambussi and Tonni, 1985*					*X*							
Tinamidae indet.										*X*		
Order Rheiformes												
Heterorhea dabbenei *Rovereto, 1914*					*X*							
Hinasuri nehuensis *Tambussi, 1995*					*X*							
Rhea americana *(Linné, 1758)*									*X*			
Rhea *sp.*								*X*		*X*		
Order Ralliformes												
Mesembriornis milneedwardsi *Moreno, 1889*					*X*							
Chunga incerta *Tonni, 1974*					*X*							
Order Gruiformes												
Porphyrio *sp.*								*X*				
Order Ciconiiformes												
Vultur gryphus *Linné, 1758*					*X*							
Dryornis pampeanus *Moreno and Mercerat, 1891*					*X*							
Order Passeriformes												
Pseudoseisura-Pseudoseisuropsis								*X*				
Motacillinae indet.								*X*				
Class Mammalia												
Order Didelphimorphia												
Thylatheridium pascuali *Reig, 1958*					*X*							
Thylamys contrerasi *Mones, 1980*					*X*							
Thylamys pusillus *(Desmarest, 1804)*										*X*		
Thylophorops *aff.* **T. perplana** *Ameghino, 1904*					*X*							
Lutreolina tracheia *Rovereto, 1914*					*X*							
Lutreolina biforata *Rovereto, 1914*					*X*							
Hyperdidelphys inexpectata *Ameghino, 1889*					*X*							
Hyperdidelphys parvula *Rovereto, 1914*					*X*							
Sparassocynus bahiai *Mercerat, 1899*					*X*							
Lestodelphys halli *(Thomas, 1921)*										*X*		
Lestodelphys *sp.*								*X*				
Order Sparassodonta												
Notocynus hermosicus *Mercerat, 1891*					*X*							
Achlysictis lelongi *Ameghino, 1891*					*X*							
Borhyaenidium *sp.*				*X*								
Order Polydolopimorphia												
Argyrolagus palmeri *Ameghino, 1904*					*X*							
Microtragulus argentinus *Ameghino, 1904*					*X*							

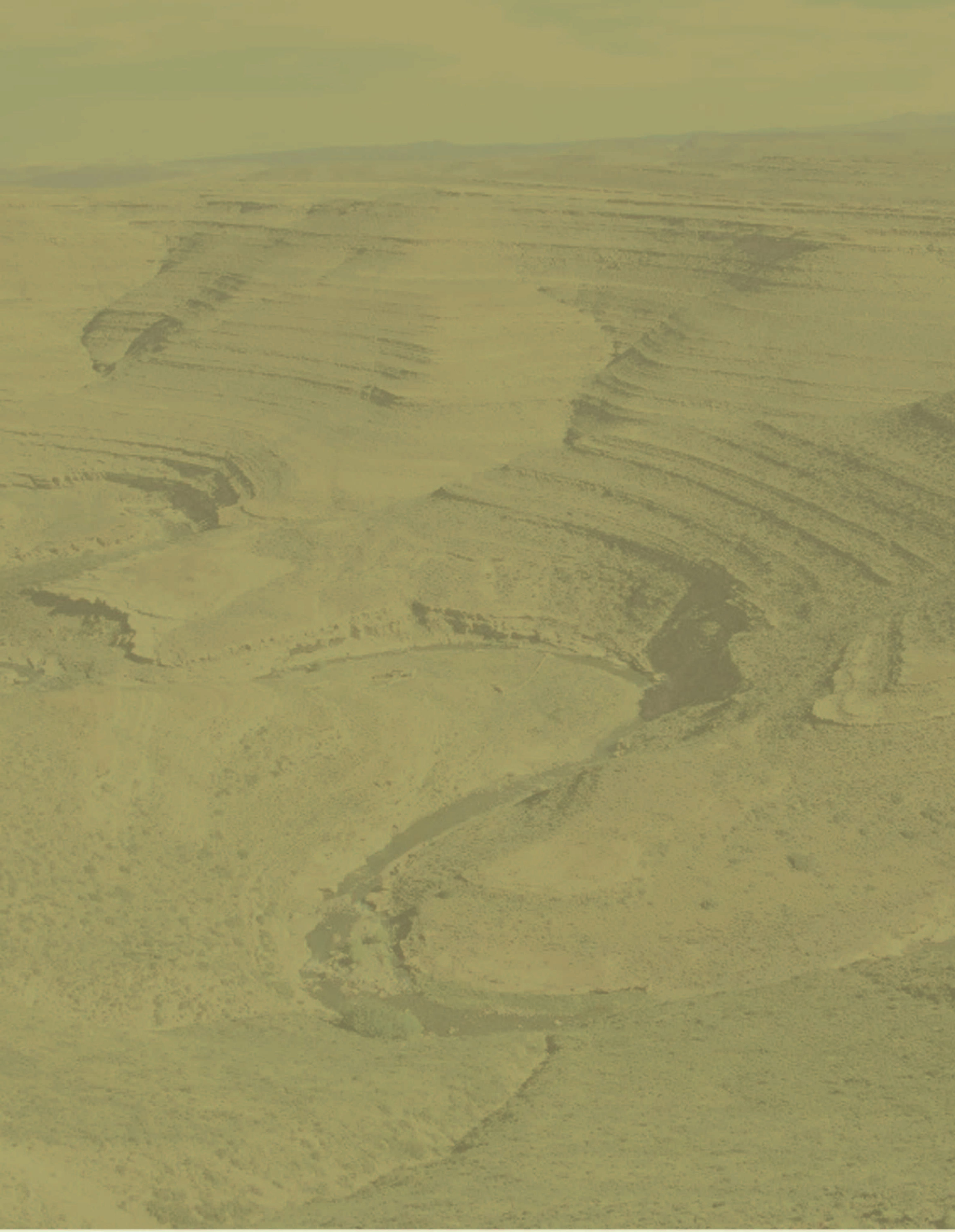
Taxa	***Localities***											
	CS	***BSar***	***CV***	***CRS***	***FMH***	***LO***	***BalS***	***BSJ***	***PLF***	***CSD***	***GdR***	***PdB***
Order Cingulata												
Euphractini sp. "a" nov. Scillato-Yané, 1982					*X*							
Holozaedyus laevisculptus *Rovereto, 1914*					*X*							
Zaedyus pichiy *(Desmarest, 1804)*								*X*	*X*	*X*		
Chaetophractus villosus *(Desmarest, 1804)*								*X*	*X*	*X*	*X*	
Tolypeutes matacus *(Desmarest, 1804)*												
Tolypeutes *sp. nov. (Scillato Yané in Deschamps, 2005)*								*X*				
Macrochorobates chapalmalensis *Scillato-Yané 1980*					*X*							
Macrochorobates *sp.*				*X*								
Chorobates villosissimus *(Rovereto, 1914)*			*X*	*X*	*X*							
Chorobates rescens *(Ameghino, 1887)*					*X*							
Chorobates *sp.*	*X*											
Macroeuphractus retusus *Ameghino, 1887*					*X*							
Macroeuphractus *cf.* **M. morenoi** *(Lydekker, 1894)*				*X*								
Propraopus *sp.*								*X*				
Eutatus seguini *Gervais, 1867*			*X*				*X*					
"Eutatus" praepampaeus *Ameghino, 1904*					*X*							
Doellotatus inornatus *(Rovereto, 1914)*	*X*				*X*							
Doellotatus *cf.* **D. praecursor** *(Rovereto, 1914)*	*X*											
Doellotatus chapadmalensis *Bordas, 1933*					*X*							
Ringueletia simpsoni *(Bordas, 1933)*					*X*							
Chasicotatus *cf.* **C. peiranoi** *Esteban and Nasif, 1996*				*X*								
Plaina *cf.* **P. intermedia** *(Ameghino, 1888)*					*X*							
Pampatherium *sp.*					*X*							
Eosclerocalyptus lineatus *Ameghino, 1888*					*X*							
Sclerocalyptus ornatus *(Owen, 1845)*			*X*									
Neosclerocalyptus *sp.*												*X*
Berthawyleria *sp.*				*X*								
Aspidocalyptus *sp.*				*X*								
Trachycalyptus *sp. nov. Scillato-Yané* et al., *1995*					*X*							
Panochthus tuberculatus *(Owen, 1839)*								*X*				
Panochthus *sp.*												*X*
Doedicurus *sp.*								*X*				
Doedicurus clavicaudatus *(Owen, 1847)*												*X*
Glyptodon clavipes *Owen, 1839*								*X*				*X*
Glyptodon reticulatus *Owen, 1845*												*X*
Nopachtus cabrerai *Zamorano* et al., *2011*					*X*							
Plohophorus figuratus *Ameghino, 1887*					*X*							
Plohophorus cuneiformis *Ameghino, 1904*					*X*	*X*						
Plohophoroides *sp.*					*X*							
cf. **Hoplophorus**							*X*					

Taxa	*Localities*											
	CS	*BSar*	*CV*	*CRS*	*FMH*	*LO*	*BalS*	*BSJ*	*PLF*	*CSD*	*GdR*	*PdB*
Phlyctaenopyga trouessarti *(Moreno, 1888)*					X							
Eleutherocercus antiquus *(Ameghino, 1887)*					X							
Palaeodaedicurus antiquus *Ameghino, 1889*					X							
Order Tardigrada												
Proscelidodon patrius *Ameghino, 1889*					X							
Scelidotherium leptocephalum *Owen, 1839*								X		X		X
Scelidotherium *cf.* **S. tarijense** *Gervais and Ameghino, 1880*												X
Glossotherium *sp.*							X	X				X
Lestodon armatus *Gervais, 1855*								X				X
Lestodon *sp.*					X							
Megatherium americanum *Cuvier, 1796*			X				X					
Myrmecophaga caroloameghinoi *Kraglievich, 1934*					X							
Order Rodentia												
Phtoramys *cf.* **P. hidalguense** *Pascual, Pisano and Ortega, 1965*	X			X								
Phtoramys homogenidens *Ameghino, 1887*					X							
aff. **Neophanomys biplicatus** *Rovereto, 1914*					X							
Neophanomys *sp.*					X							
Pithanotomys columnaris *Ameghino, 1887*					X							
Pithanotomys macer *Ameghino, 1888*					X							
Pseudoplataeomys formosus *Kraglievich, 1934*					X							
Eucelophorus cabrerai *Kraglievich, 1927*					X							
Xenodontomys ellipticus *Kraglievich, 1927*	X	X	X									
Actenomys priscus *(Owen, 1840)*					X	X						
Eumysops laeviplicatus *Ameghino, 1888*					X							
Eumysops formosus *Ameghino, 1906*					X							
Ctenomys talarum *Thomas, 1898*							X			X	X	
Ctenomys *sp.*										X		
Ctenomys kraglievichi *(Rusconi, 1930)*								X				
Myocastor columnaris *Rusconi, 1929*								X				
Paramyocastor diligens *(Ameghino, 1888)*					X							
Lagostomus incisus *(Ameghino, 1888)*					X							
Lagostomus *sp.*	X	X				X	X	X				
Lagostomus maximus *(Desmarest, 1817)*												
Palaeocavia *sp.*	X	X			X							
Neocavia depressidens *Parodi and Kraglievich, 1948*					X							
Neocavia *sp.*					X							
Dolicavia *sp.*						X						
Galea *sp.*			X									
Microcavia *sp.*					X			X				
Cavia aperea *Erxleben, 1777*				X	X	X						
Orthomyctera sp.	X				X	X						

Taxa	*Localities*											
	CS	*BSar*	*CV*	*CRS*	*FMH*	*LO*	*BalS*	*BSJ*	*PLF*	*CSD*	*GdR*	*PdB*
Prodolichotis *sp.*					*X*							
Caviodon australis *(Ameghino, 1888)*					*X*							
Cardiomys *sp.*					*X*							
Phugatherium cataclisticum *Ameghino, 1889*					*X*							
Neochoerus *cf.* **N. tarijensis** *(Ameghino, 1902)*								*X*				*X*
Telicomys giganteus *Ameghino, 1904*					*X*							
Phyllotini gen. et sp. nov. Bond et al., 1998					*X*							
Necromys bonapartei *(Reig, 1978)*					*X*							
Auliscomys formosus *Reig, 1978*					*X*							
Reithrodon auritus *(Fischer, 1814)*					*X*			*X*		*X*		
Lundomys *sp.*								*X*				
Holochilus brasiliensis *(Desmarest, 1819)*										*X*		
Akodon azarae *(Fischer, 1829)*								*X*				
Akodon iniscatus *Thomas, 1919*								*X*				
Oxymycterus *sp.*								*X*				
Calomys laucha *(Fischer, 1814)* - **C. musculinus** *(Thomas, 1913)*										*X*		
Phyllotis *sp.*								*X*				
Order Lagomorpha												
Lepus europaeus *Linné, 1758*							*X*					
Order Notoungulata												
Paedotherium bonaerense *Ameghino, 1887*		*X*			*X*		*X*					
Paedotherium typicum *Ameghino, 1887*					*X*							
Paedotherium *cf.* **P. minor** *Cabrera, 1937*	*X*			*X*								
Paedotherium *sp.*			*X*									
Tremacyllus impressus *Ameghino, 1888*	*X*				*X*							
Tremacyllus *cf.* **T. impressus**				*X*								
Hemihegetotherium *sp.*												
Pseudotypotherium *sp.*					*X*	*X*						
Toxodon chapalmalensis *Ameghino, 1908*					*X*							
Toxodon platensis *Owen, 1837*			*X*				*X*					
Alitoxodon vetustum *Rovereto, 1914*					*X*							
Trigodon gaudryi *Ameghino, 1882*					*X*							
Trigodon minor *Rovereto, 1914*					*X*							
Xotodon prominens *Ameghino, 1889*					*X*							
Xotodon ambrosetti *Rovereto, 1914*					*X*							
Xotodon *sp.*					*X*							
Order Litopterna												
Eoauchenia primitiva *Ameghino, 1887*					*X*							
Epitherium laternarium *Ameghino, 1888*					*X*	*X*						
Diplasiotherium robustum *Rovereto, 1914*					*X*							
Promacrauchenia antiqua *Ameghino, 1889*					*X*							

Taxa	*Localities*											
	CS	*BSar*	*CV*	*CRS*	*FMH*	*LO*	*BalS*	*BSJ*	*PLF*	*CSD*	*GdR*	*PdB*
Promacrauchenia kraglievichi *Parodi, 1931*					*X*							
Promacrauchenia *sp.*				*X*								
Macraucheniopsis ensenadensis *(Ameghino, 1888)*								*X*				
Macrauchenia patachonica *Owen, 1838*										*X*		*X*
Order Proboscidea												
Notiomastodon platensis *(Ameghino, 1888)*												*X*
Gomphotheriidae indet.								*X*				
Order Artiodactyla												
Tayassuinae indet.								*X*				
Lama *sp.*								*X*				
Lama guanicoe *(Müller, 1776)*							*X*			*X*	*X*	
Ozotoceros bezoarticus *(Linné, 1758)*									*X*	*X*		
Morenelaphus bonaerense *Carette, 1922*												*X*
Ovis aries *Linné, 1758*									*X*	*X*		
Bos taurus *Linné, 1758*									*X*	*X*		
Order Perissodactyla												
Equus (Amerhippus) neogaeus *Lund, 1840*										*X*		*X*
Hippidion principale *(Lund, 1846)*								*X*				
Hippidion *sp.*												*X*
Order Carnivora												
Parahyaenodon argentinus *Ameghino, 1904*					*X*							
Tetraprothomo argentinus *Ameghino, 1908*					*X*							
Cyonasua clausa *Ameghino, 1904*					*X*							
Smilodon populator *Lund, 1842*												*X*
Pseudalopex *sp.*								*X*				
Pseudalopex gymnocercus *(Fischer, 1814)*										*X*		
cf. **Herpailurus**								*X*				

BalS, Balneario Saldungaray; **BSar,** Barrancas de Sarmiento; **BSJ,** Bajo San José; **CSD,** Chacra Santo Domingo; **CRS,** Cantera Relleno Sanitario; **CS,** Cantera Seminario; **CV,** Cantera Vialidad; **FMH,** Farola Monte Hermoso; **GDR,** García del Río; **LO,** Las Oscuras; **PdB,** Playa del Barco; **PLF,** Puesto La Florida.



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