

Biotic assemblages from Early Cretaceous lacustrine systems in the San Luis Basin, mid-western Argentina

A. Arcucci⁽¹⁾, M. B. Prámparo⁽²⁾, L. Codorniú⁽³⁾, G. Giordano⁽³⁾, G. Castillo-Elías⁽¹⁾, G. Puebla⁽²⁾, N. Mego⁽²⁾, M. A. Gómez⁽¹⁾ y E. Bustos-Escalona⁽¹⁾

(1) Área de Zoología, Dep. de Bqca y Cs. Biológicas, Universidad Nacional de San Luis, Chacabuco 917, 5700, San Luis Argentina. andrea.arcucci@gmail.com

(2) CCT CONICET Mendoza – IANIGLA – Bajada del cerro s/n, 5500, Mendoza, Argentina.

(3) CONICET Depto de Geología, Universidad Nacional de San Luis, Av. Ejército de los Andes 950, 5700 San Luis, Argentina.

ABSTRACT

Significant paleobiological data has emerged from the San Luis Basin (Early Cretaceous, Aptian-Albian in Central Argentina) during the last decades. Two units in this basin include lake paleo-environments with important fossil contents in an excellent state of preservation that could be considered as *Konservat Lagerstätten* deposits. The association of fossil leaves and pollen grains from the La Cantera Formation is one of the most ancient and complete angiosperm records in South America and the bryophyte association of the same unit constitutes one of the most complete records of its type in Argentina. Insects from five different orders have been identified in this association, and three endemic species of aquatic insects from the La Cantera Formation have been described as belonging to the Notonectidae and Corixidae families, including the oldest member of the Anisopinae subfamily. The *Pterodaustro guinazui* association from the Lagarcito Formation is one of the few fossil associations recorded worldwide from which it is possible to make studies on the life history parameters of pterosaurs-like growth patterns and ontogeny. The Pleuropholid fish from the Lagarcito Formation are the only record of this group in Argentina and the second in South America. Several new species of ostracods and conchostracea have also been recorded from the same units. Despite the amount of paleontological information now available from the San Luis basin, much work remains to be done on these fossil associations and the interpretation of their depositional environments.

Keywords: angiosperms, Aptian-Albian, Early Cretaceous, Notonectidae insects, pterosaurs.

Asociaciones bióticas de los sistemas lacustres del Cretácico Temprano de la Cuenca de San Luis, centro oeste de Argentina

RESUMEN

Abundante información paleobiológica relevante ha surgido en las últimas décadas de la Cuenca de San Luis (Cretácico Temprano del centro de Argentina). Dos unidades geológicas en esta cuenca incluyen ambientes lacustres con un diverso contenido fósil y una excelente conservación que puede considerarse como depósitos de tipo Konservat Lagerstätten. La asociación de restos vegetales y granos de polen de la Formación La Cantera es uno de los registros más antiguos y completos con angiospermas en América del Sur, con la presencia de otros grupos como las briofitas en los mismos niveles, que constituyen uno de los registros más completos de su tipo en Argentina. Insectos pertenecientes a cinco órdenes diferentes fueron identificados en esta asociación, y tres especies endémicas provienen de la Formación La Cantera, de las familias Notonectidae y Corixidae, incluyendo el miembro más antiguo de la subfamilia Anisopinae. La asociación de Pterodaustro guinazui de la Formación Lagarcito es uno de los escasos registros mundiales de pterosaurios donde es posible estudiar patrones de crecimiento y ontogenia de estos arcosaurios. Los peces Pleuropholidae de la misma formación son un registro único en Argentina y el segundo de su tipo en América. Varias especies de ostrácodos y conchostracos han sido registradas en estas mismas unidades. A pesar de la cantidad de información paleontológica existente proveniente de la cuenca de San Luis, mucho trabajo queda por realizar sobre estas asociaciones fósiles así como sobre la interpretación de sus ambientes depositacionales.

Palabras clave: angiospermas Aptiense-Albiense, Cretácico Temprano, insectos Notonéctidos Pterosaurios.

VERSIÓN ABREVIADA EN CASTELLANO

Introducción

El contenido fosilífero de la Cuenca de San Luis se conoce desde hace más de tres décadas pero no había sido sistemáticamente explorado ni estudiado en profundidad hasta hace pocos años. La mencionada cuenca se ubica en una posición geográfica relevante, ya que es la única que incluye niveles fosilíferos lacustres cretácicos, localizada fuera de la Patagonia, en Sudamérica. En ella, dos unidades dentro del Grupo El Gigante, las Formaciones La Cantera y Lagarcito, registran ambientes continentales del intervalo Aptiense-Albiense. El registro conocido incluye palinomorfos, restos macroflorísticos, invertebrados y vertebrados en un excelente estado de conservación. La Formación La Cantera está compuesta de arcilla y limolita gris-verdosas con arenisca fina intercaladas y arcilla rojiza hacia el tope de la sección que consta de aproximadamente 31 metros de espesor en su localidad tipo, en la Sierra del Gigante (Figura 1). Estos sedimentos representarían lagos temporarios relacionados con ambientes fluviales con algunos períodos de cuerpos de agua estables (Flores and Criado Roque, 1972) que permitieron la conservación de estructuras orgánicas delicadas. Basados en los estudios palinológicos, la edad sugerida para estos niveles es Aptiense superior (Prámparo 1990, 1994, 1999a; Prámparo et al., 2007). La Formación Lagarcito (Figura 2), corresponde a sedimentos silicoclásticos fluvio-lacustres (Rivarola and Spalletti, 2006), depositados en una alternancia de limolita y arcilla rojiza y verdosa en una sección con un espesor que varía entre 100 y 400 m. Chiappe et al. (1998a) asignaron una edad albiana a esta unidad en su localidad tipo en la Sierra de las Quijadas (Figura 1), basándose en su contenido fosilífero y en dataciones (K-Ar) de 107.4-109.4 M.a. (Yrigoyen, 1975) para los basaltos de la suprayacente Formación La Cruz. Prámparo et al. (2005) describieron registros de la Formación Lagarcito en la Sierra de Guayaguas y acordaron con esa edad albiana en base a la presencia de esporas verrugosas también registradas en el Cretácico Temprano de Brasil (Mego and Prámparo, 2013). Estudios sedimentológicos muestran que las facies fosilíferas de la Formación Lagarcito en la Sierra de las Quijadas fueron depositadas en un lago perenne somero de agua dulce situado en una llanura aluvial en condiciones semiáridas predominantes (Chiappe et al., 1998a). La diversidad de las asociaciones fosilíferas es notable, aunque la abundancia y la conservación de los especímenes varían entre las diferentes localidades de cada unidad (Chiappe et al., 1998a, b; Arcucci et al., 2009). Estas asociaciones pueden ser consideradas en muchos aspectos como Konservat-Lagerstätten, o sitios de preservación excepcional donde la información paleontológica ha sido conservada de manera especial, incluyendo partes blandas. El objetivo de este artículo es presentar los hallazgos más recientes de los diferentes grupos registrados en estas unidades lacustres del Aptiense-Albiense (Formaciones La Cantera y Lagarcito) en la Cuenca de San Luis en el Centro Oeste de Argentina, incluyendo identificaciones e interpretaciones actualizadas de tales asociaciones.

Resultados

La macroflora de la Formación La Cantera se encuentra caracterizada por la predominancia de angiospermas (restos de hojas y estructuras reproductivas como semillas y flores). Entre los restos de angiospermas, se encuentra un morfotipo que representa el registro más antiguo de hojas compuestas (Puebla, 2009) (lámina 1, Figuras 16 y 17). El polen de angiospermas, en cambio, en general está presente en bajos porcentajes (Prámparo 1990b). Los géneros hallados son *Afropollis*, *Retimonocolpites* sp., *Stellatopollis* sp., *Clavatipollenites* sp., *Tucanopollis*, *Pennipollis* y el complejo *Asteropollis*. El registro asimismo incluye impresiones de pequeño tamaño y compresiones de fragmentos de esfenofitas (equisetales), briofitas, pteridofitas y gnetofitas (*Ephedra*) (Puebla, 2009, 2010; Puebla et al., 2012). Las muestras de la Formación Lagarcito provienen de la Sierra de Guayaguás, en la provincia de San Juan (Figura 1). Estudios palinológicos (Prámparo and Milana, 1999; Prámparo et al., 2004, 2005) indican una palinoflora dominada por gimnospermas (granos plicados y rimulados). Entre ellos, polen de diferentes especies de *Cycadopites* y *Ephedripites* son los elementos más frecuentes. Las esporas triletes están bien representadas así como las esporas verrugosas (Mego and Prámparo, 2013). Los vertebrados de la Formación La Cantera están representados solamente por peces actinoptergios, incluidos en dos grandes grupos. Por un lado, especímenes de actinoptergios basales de unos 10 cm de longitud total (lámina 2, Figuras 1 y 2), que fueron preliminarmente interpretados como afines a condrosteos o a coccolepidos según diferentes autores (López-Arbarello et al., 2002a, López-Arbarello, 2004; Castillo-Elías, 2011). Por otro lado, se hallan especímenes de un neoptergio basal provisto de escamas ganoideas y de 5 cm de longitud total (lámina 2, Figuras 3 y 4). Durante los últimos años, gran cantidad de nuevo material referido a ambos grupos ha sido colectado y se encuentra actualmente bajo estudio, intentando clarificar sus respectivas afinidades filogenéticas. Los vertebrados de la Formación Lagarcito incluyen peces y una especie de pterosaurio. Entre los primeros, la mayoría de los especímenes pertenecen a Semionotiformes (lámina 2, Figura 5) con *Neosemionotus puntanus* Bocchino, 1973 como el único taxón vál-

do (López-Arbarello y Codorníu, 2007). El registro de peces de esta formación incluye otro taxón de actinopterio identificado como Pleuropholidae (lámina 2, Figura 6). Pterodaustro guinazui (Bonaparte, 1970) es un pterosaurio con numerosos dientes filtradores del que se han colectado cientos de especímenes en esta localidad fosilífera (Chiappe et al., 1998a, b). Dentro de la muestra colectada hay pocos ejemplares completos y articulados (lámina 3), pero una gran abundancia de especímenes parcialmente articulados o aislados, incluyendo alas articuladas, huesos largos de los miembros posteriores, vértebras y cinturas, todos ellos referidos a una única especie debido a sus particulares características anatómicas. La muestra que provee la Formación Lagarcito es única en América del Sur y representa a cientos de individuos con una amplitud de ala de entre 30 cm a 3 m, incluyendo un espécimen de embrión dentro de fragmentos de un huevo (Chiappe et al., 2004, Codorníu, 2005) y aún está siendo estudiada. El registro de invertebrados fósiles de la Formación La Cantera muestra una variedad de artrópodos incluyendo insectos y crustáceos. Varias décadas transcurrieron desde los primeros hallazgos de insectos (Flores, 1969) hasta que se realizaron estudios sistemáticos (Mazzoni and Hünicken, 1984, 1987) y se reconocieron dos familias de insectos acuáticos, Notonectidae y Corixidae, con dos nuevas especies: *Canteronacta irajae* y *Romboidella popovi*. Siete Familias que pertenecen a cinco Órdenes de insectos fueron identificadas posteriormente: Orthóptera, Coleóptera, Hemíptera, Glosselytropea y Neuróptera. Petrulevicius et al. (2005, 2010) analizaron la paleoecología de esta asociación de insectos, describiendo una nueva especie, *Notonecta mazzoniae*. De igual forma los mismos autores registraron la presencia del miembro más antiguo de Anisopinae (Familia Notonectidae) en América del Sur. Entre los hallazgos de crustáceos en la Formación La Cantera están presentes ostrácodos y conchostracos aun indeterminados. En la Formación Lagarcito se encontraron conchostracos y ostrácodos asociados a palinómorfos y algas clorofíceas (Prámparo et al. 2005). En la localidad de la Sierra de Guayaguas, fueron identificadas tres especies de conchostracos, dos de ellas nuevas: *Estheriina aff. E. astartoides*, *Pseudestherites rivarolai* Gallego (in Prámparo et al., 2005) y *Dendrostracus lagarcitoensis* Gallego (in Prámparo et al., 2005) También fueron identificadas y descritas once especies de ostrácodos pertenecientes a siete géneros, incluidas a su vez en cinco familias: Candona, Lymnocypridea, Cypridea, Mongolianella, Petrobrasia, Clinocypris, y Darwinula.

Conclusiones

La asociación fosilífera de angiospermas de la Formación La Cantera constituye uno de los registros más antiguos y completos de sus primeros representantes en América del Sur. La asociación de briófitas de la misma unidad constituye asimismo la más completa registrada en el Mesozoico de Argentina. La diversidad de insectos, pertenecientes a cinco órdenes, es una de las más altas conocidas para este período. Las tres especies endémicas de insectos acuáticos descritas procedentes de los niveles de La Cantera pertenecen a Notonectidae y Corixidae y son los más antiguos de Argentina. De igual forma se encuentra registrado el único miembro de la subfamilia Anisopinae en América del Sur. Pterodaustro guinazui de la Formación Lagarcito constituye uno de los escasos registros mundiales de pterosaurios que permite aproximarse a la historia de vida de estos animales y a sus patrones de crecimiento y a su ontogenia. Los pleuropholidos de la misma formación son el primer registro de estos peces en Argentina y el segundo en América. La gran cantidad de información disponible actualmente proveniente de estas Formaciones cretácicas de la Cuenca de San Luis, permitirá desarrollar mejores interpretaciones de la geología y los ambientes sedimentarios de estas unidades y reconstrucciones de la paleobiología de los diferentes grupos de organismos registrados y de los ambientes donde vivieron.

Introduction

The Cretaceous San Luis Basin is located in mid-western Argentina (between 31 to 33° south latitude), with outcropping sections in the San Luis (Sierra del Gigante, Sierra de Las Quijadas) and San Juan provinces (Sierra de Guayaguas) (Fig. 1). It is represented by the continental sediments of the El Gigante Group (Los Riscos, El Jume, La Cantera, El Toscal, La Cruz and Lagarcito Formations) (Fig. 2). These units correspond to the continental infilling of an extensional

basin, related to the breakup of Gondwana during the Cretaceous (Rivarola and Spalletti, 2006). The El Gigante group is one of the most paleontologically productive continental cretaceous successions in Argentina. The fossiliferous content from San Luis Basin has been known for more than 30 years, though it was not systematically explored until the last decade. Its geographic position is relevant because it is the only basin with lacustrine fossiliferous beds located outside Patagonia in southern South America, recording the continental ecosystems for the Aptian-

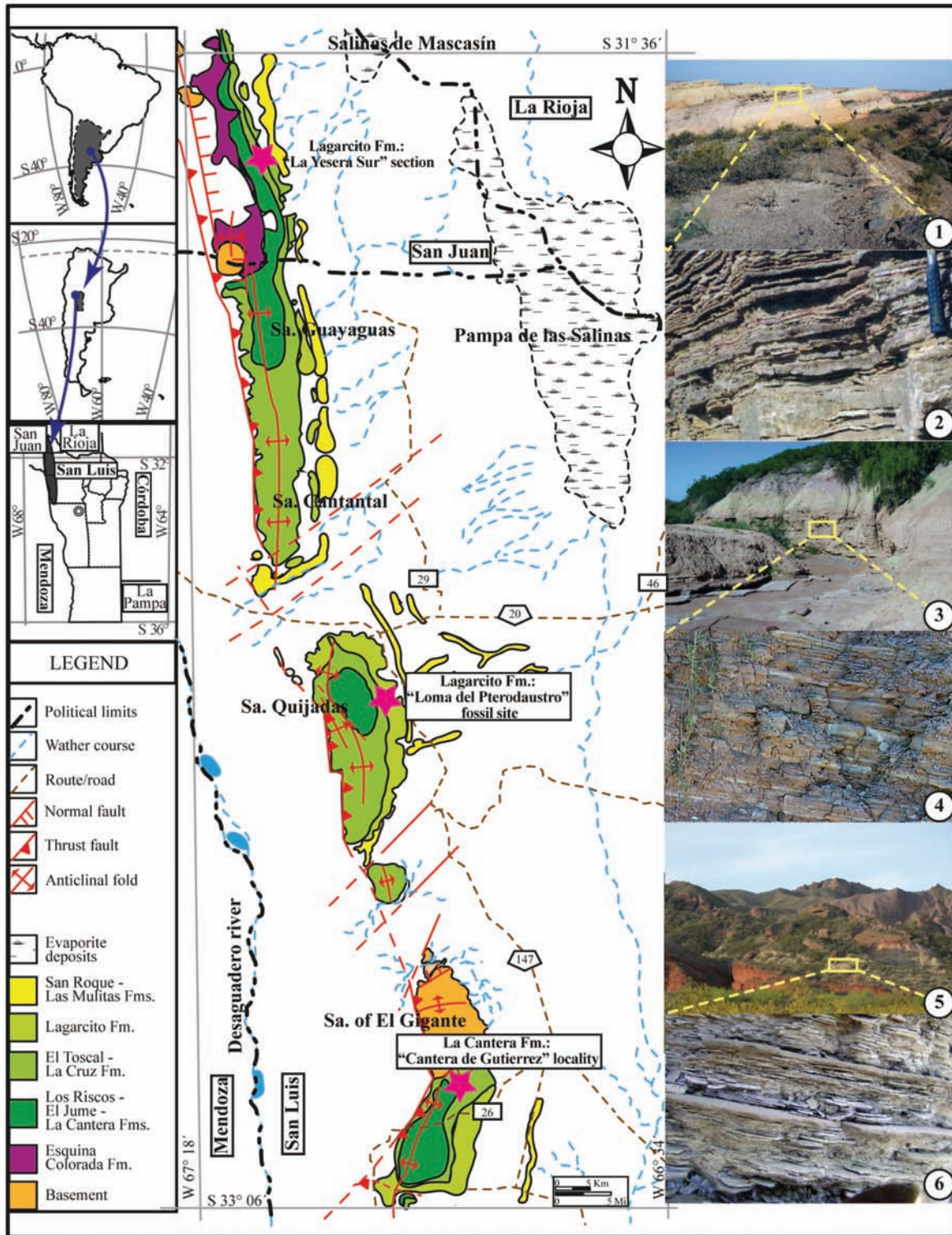


Figure 1. Location map of the San Luis Basin showing all fossil locations. Photos 1-2: panoramic view of "La Yesera Sur" section (Lagarcito Fm.) with a zoom of the fossiliferous layers. Photos 3-4: Panoramic view of the "Loma del Pterodaustro" fossil site (Lagarcito Fm.) with a zoom of the fossiliferous layers. Photos 5-6: Panoramic view of "Cantera de Gutierrez" location (La Cantera Fm.) with a detail of the fossiliferous layers.

Figura 1. Mapa de ubicación de la Cuenca de San Luis mostrando todas las localidades fosilíferas. Fotos 1 y 2: Panorámica de la sección "La Yesera Sur" (Formación Lagarcito) con un acercamiento de los niveles fosilíferos. Fotos 3 y 4: Panorámica del sitio "Loma del Pterodaustro" (Formación Lagarcito), con un acercamiento de los niveles fosilíferos. Fotos 5 y 6: Panorámica de la localidad "Cantera de Gutierrez" (Formación La Cantera) con un detalle de los niveles fosilíferos.

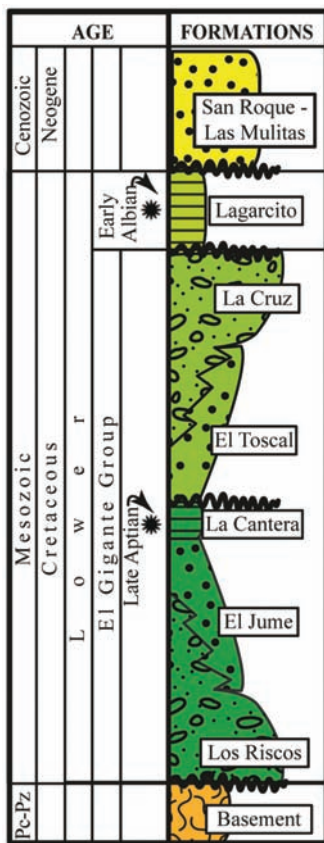


Figure 2. Generalized stratigraphic column showing all the areas of study. Pc-Pz: Precambrian - Paleozoic.

Figura 2. Columna Estratigráfica generalizada mostrando las unidades del área de estudio. Pc-Pz: Precámbrico - Paleozoico.

Albian interval and including palynomorphs, macrofloristic remains, invertebrates and vertebrates in a very good state of preservation. The diversity of the fossil associations is also remarkable although the abundance and preservation of the specimens vary among the different units and localities (Chiappe *et al.*, 1998b, Arcucci *et al.*, 2009). These assemblages could be considered, in many aspects, as *Konservat-Lagerstätten*, or sites where exceptional palaeobiological information has somehow been preserved. The occurrence of particular events of mass mortality and rapid burial are the usual explanations for these exceptional deposits (Seilacher, 1990, Buscalioni and Fregenal Martínez, 2010).

In this paper we present a compilation with an update of the paleontological studies developed in the last decade on each group of organisms in these assemblages within the geological frame available at present. The different fossil groups recovered from the lacustrine cretaceous units are presented with a

discussion of the systematic composition, including a complete revision of previous studies. The aim of this paper is to present for the first time the complete record of the different fossil groups studied from the Aptian-Albian lacustrine units (La Cantera and Lagarcito Formations) in the San Luis Basin, in mid-western Argentina, including new identifications and current interpretation of these assemblages. A complete list of the species mentioned in the manuscript is included at the end of the paper.

The fossil specimens studied are deposited in the following institutions:

Institutional abbreviations: MIC, 'Contacto', Museo Interactivo de Ciencias, UNSL, San Luis; Paleopalintoteca del Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA, CONICET) Mendoza, MPLP (Mendoza – Paleopalintoteca - Laboratorio de Paleopalintología).

Geological setting and stratigraphic framework

Several basins of mid-western Argentina were active from the Triassic, but during the Cretaceous a new activation produced a new stage of *rifting*, which has its greater development and importance from north to south (Uliana and Biddle, 1988). The Cretaceous extensional system (Patagonidic extension), was linked to the breakup of Gondwana, with the opening of the South Atlantic Ocean during the Early Cretaceous and it was preceded by prominent Triassic extensional systems. The San Luis Basin would have filled within the Aptian-Albian stage and it is part of the so-called rift basins in rosary of north-northwest direction or the "western Cretaceous rift system" (Rossello and Mozetic, 1999). This basin is located in the southwest margin of the geological province of the Sierras Pampeanas, in the northwest of San Luis province (Flores and Criado Roque, 1972; Yrigoyen, 1975). The San Luis Basin had several active depocentres during the Early Cretaceous: Sierra de Guayaguas (La Yesera Sur section), Sierra de Las Quijadas ("Loma del Pterodaustro" fossil site), Sierra de El Gigante ("Cantera de Gutierrez" locality) (Fig. 1). As a result of this reactivation of the basin the infilling was generated in a first step with *synrift* deposits corresponding to the El Gigante Group, culminating with the deposition of the Lagarcito Formation in a *sag* stage (Schmidt *et al.*, 1995). The sedimentary rocks of the El Gigante Group are composed of conglomerates, sandstone and mudstone deposited in alluvial fan palaeoenvironments. In Sierra de las Quijadas (Chiappe *et al.*, 1998a) they are associated with fluvial systems, lake and mud flat deposits and occasional

intercalations of eolian sandstone. In this area Rivarola and Spalletti (2006) divided the El Gigante Group in two fining upward sequences, each with different architecture and lithofacies compositions. The lower sequence is composed of Los Riscos, El Jume and La Cantera formations; and the upper sequence of El Toscal, La Cruz and Lagarcito formations (Fig. 2). The sedimentary record is made up of proximal alluvial fan facies that pass downstream into ephemeral fluvial facies and mudflat/lacustrine facies. The La Cantera and Lagarcito formations mainly correspond to lacustrine fine deposits. These units have yielded relevant paleontological assemblages with some interesting diversity and exceptional conditions of preservation that are presented here.

La Cantera Formation is composed of laminated green-grey mudstone, siltstones and claystone, with red-brown sandstone and grey siltstones interbedded at the top of the succession. The thickness at its type locality is 31 metres (Sierra del Gigante) (Fig. 1). It may represent ephemeral lakes related to a fluvial environment with some periods of a very quiet lacustrine system (Flores and Criado Roque, 1972), which allowed the preservation of delicate structures such as leaves, stems and flowers. Primary gypsum is interbedded with clastic sediments several times in the section. Based on palynological studies, the age suggested for these levels is Late Aptian (Prámparo 1990, 1994, 1999a, b, Prámparo *et al.*, 2007). In the "Cantera de Gutierrez" location the sequence begins with the deposition of the El Gigante Group (Kr) on the top of the basement of the "Complejo metamórfico El Gigante" (Pc-Lw. Pz). Two fining upward sequences are deposited, the lower sequence is made up of the Los Riscos, El Jume and La Cantera formations; and the upper sequence by the El Toscal and La Cruz formations. The La Cantera Formation is composed of siliclastic and evaporitic sedimentary sequences, and has two different members. The lower member is mainly composed of laminated mudstones and siltstones interbedded, with the primary gypsum subordinated. The upper member is predominantly composed of claystones and primary gypsum and the siltstones are subordinated. Preliminary interpretations indicate that it may be principally a detritic lake with some evaporite levels, which had variable hydrologic conditions. So far almost all the formation levels are fossiliferous, the majority being located in the lower member. The section culminates with the deposition of the San Roque Fm. (Neogene) and quaternary loess.

The Lagarcito Formation, within the El Gigante Group (Fig. 2) corresponds to siliclastic fluvio-lacustrine sediments (Rivarola and Spalletti 2006), com-

posed of an alternating of reddish and greenish mudstones and fine sandstone in a section with a thickness varying from 100 to 400m. Chiappe *et al.*, (1998a, b) assigned an Albian age to the Lagarcito Formation at its type locality (Sierra de las Quijadas) (Fig. 1), based on its fossil content and the K-Ar dates of 107.4-109.4 My (Yrigoyen, 1975) for the basalts of the La Cruz Formation. Prámparo *et al.*, (2005) described the only paleontological record of the Lagarcito Formation at the Sierra de Guayaguas and agreed with the Albian age based on the presence of verrucose spores with affinities with those recorded in the Brazilian Early Cretaceous basins (Mego and Prámparo, 2013). Sedimentological studies show that the absence of evaporitic sediments and the lack of evidence of subaerial exposition indicate that the fossil-bearing facies of the Lagarcito Formation in the Sierra de Las Quijadas were deposited in a perennial freshwater shallow lake, situated in an alluvial plain where semiarid climate conditions predominated (Chiappe *et al.*, 1998a). In the "La Yesera" section (Fig. 2) the sequence begins with the deposition of proximal conglomerates from the Quebrada del Barro Fm. (Upper Triassic) on the top of the basement of the "Valle Fértil Group" (Pc-Lw. Pz). During the Cretaceous a new phase of rifting was superimposed and Los Riscos, El Jume, El Toscal y La Cruz formations were deposited, culminating with the deposition of the Lagarcito Formation. This last unit covers a large area meridionally elongated of outcrops that ends in Marayes to the North, and corresponds to a reddish psamopelitic-evaporitic succession with interbedded gypsum and anhydrite usually at the bottom. Various types of lacustrine and fluvial environments have been recorded in the studied section, from a meromictic shallow lake with low salinity to a shallow stratified lake to sabhka saline deposits. The fluvial systems are ephemeral transitional to lacustrine systems. Seven lacustrine episodes have been detected throughout the section, but numerous fossils were only found in the first three. The section culminates with the deposition of the San Roque Formation (Neogene) and quaternary loess. In the "Loma del Pterodaustro" section the sequence begins with the deposition of the El Gigante Group (Kr) in two fining upward sequences, the lower sequence composed of the Los Riscos and El Jume formations; and the upper sequence by the El Toscal, La Cruz and Lagarcito formations. The Lagarcito Formation in this site is composed of siliclastic and evaporitic sedimentary sequences corresponding to typical red beds, however the multifacial and varicoloured character of its rocks stands out. The environment corresponds to a lacustrine depositional sys-

tem with perennial characteristics, which, in a subordinate manner, combined with an ephemeral lacustrine depositional system, another tributary fluvial of the lake. To a lesser extent the presence of a single level of sediments of eolic origin has been determined. So far we have identified three fossiliferous levels. The section culminates with the deposition of the San Roque Formation (Neogene) and quaternary loess.

A generalized stratigraphic column of the studied units is shown in Figure 2.

Fossil assemblages

A) Plant macrofossils and palynomorphs

The La Cantera Formation at its type locality (Cantera de Gutierrez, Sierra del Gigante) (Fig.1) has provided one of the most ancient and complete associations of pollen grains and plant remains, including primitive angiosperms, which allows us to consider the unit as Late Aptian in age. The macroflora is characterized by the predominance of angiosperms with a low representation of other groups. The record of this unit includes small impressions and compressions of angiosperm leaves, fragments of sphenophytes (equisetalean), bryophytes, pteridophytes, gnetophytes (*Ephedra*) and diverse types of reproductive structures such as seeds, cones and flowers (Puebla, 2009, 2010; Puebla *et al.*, 2012). Among the angiosperm remains one of the morphotypes studied, "LC Microphyll trifoliolate" (see complete description in Puebla, 2009) represents the earliest record of pinnately compound leaves (Plate 1, Figs. 16, 17). It can also be considered as allied to the eudicots, being among the earliest leaf records within this group (Archangelsky *et al.*, 2009). The La Cantera Formation has also yielded an important fossil plant association (disperse spores and macroscopic remains) belonging to Bryophyta, mainly with hepatic affinity. The palynoflora is dominated by aquatic forms (fresh water algae) in nearly all the assemblages studied (Prámparo 1990, 1999b). In some levels of the sections they make up more than 80% of the total population. The gymnospermous elements are mainly represented by plicate and rimulate grains. Different species of *Ephedripites/Stevesipollenites* of gnetalean affinity are frequently together with monosulcate grains of the genera *Cycadopites* and *Monosulcites*. *Classopollis* grains are abundant (30%) in some levels. Trilete spores are very scarce, only represented by some species of *Cicatricosisporites* and *Appendicisporites* (Prámparo, 1989; Narváez *et*

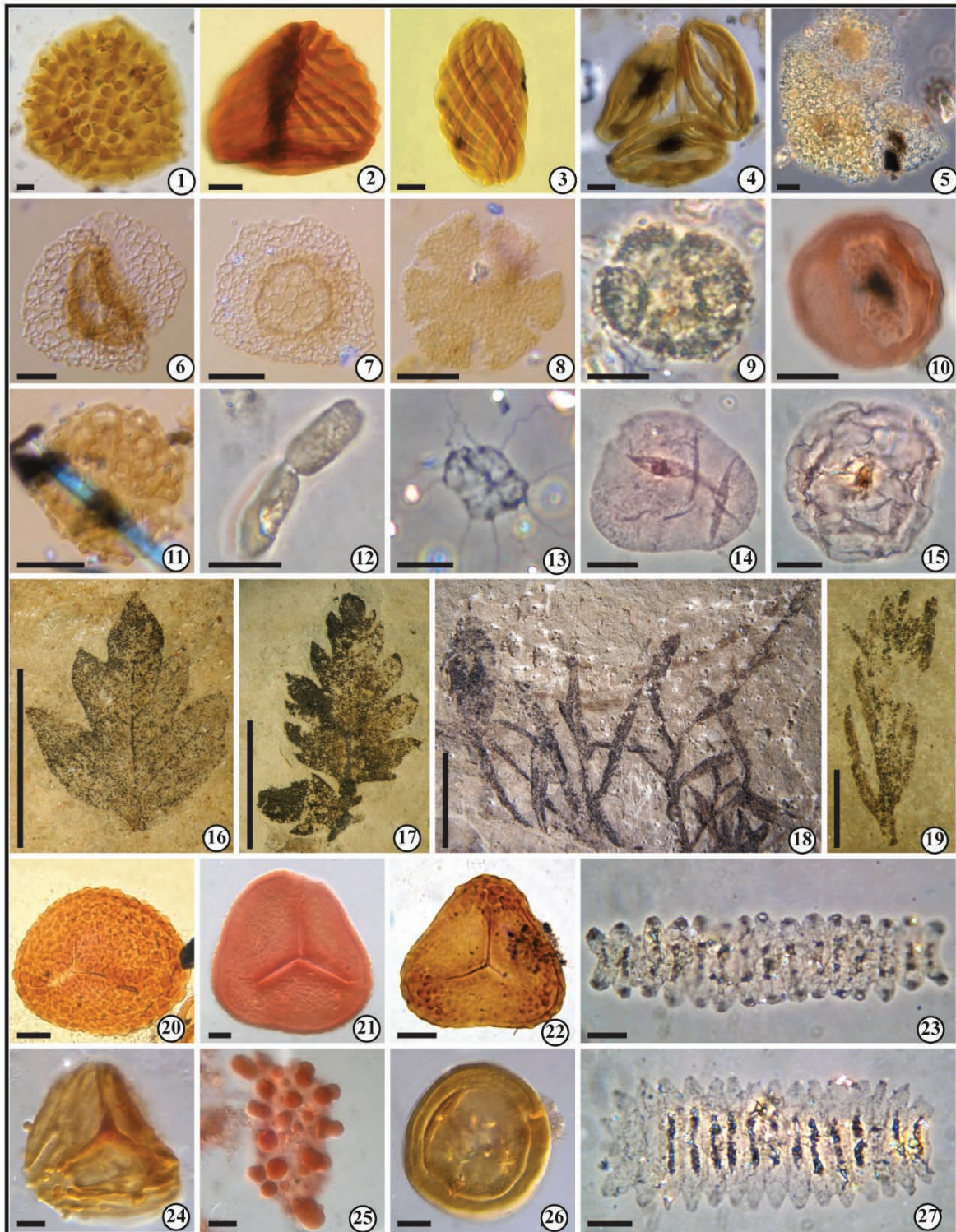
al., 2013); less significant in number are the spores of *Crybelosporites* sp. and the hilates such as *Couperisporites* cf. *complexus*, *Aequitriradites* cf. *verrucosus*, *Foraminisporis asymmetricus*, *Zlavisporis reticulatus* and *Coptospora* spp (Puebla *et al.*, 2012). Bisaccate grains are also scarce. The angiosperms are present in low percentages and they become more representative at the top of the studied sections (Prámparo 1999a). The genera found are *Afropollis* (*A.operculatus*, *A.zonatus*, *A. aff. jardinus*), *Retimonocolpites* sp., *Stellatopollis* sp., *Clavatipollenites* sp., *Tucanopollis*, *Pennipollis* (ex *Brenneripollis*) *peroreticulatus* and *Asteropollis* complex (*Stephanocolpites mastandreai/Huitrinipollenites transitorius*).

Chiappe *et al.*, (1998a, b) described the first plant remains from the Lagarcito Formation recovered from Sierra de Las Quijadas, in the main fossiliferous locality (Fig. 1). This record is an imprint with very limited relief and no preserved organic matter, which suggests some kind of reproductive structure that they assigned to the "Magnoliophyta indet". Prámparo *et al.*, (2005) described the only micropaleontological record of Lagarcito Formation at the locality of Sierra de Guayaguás. The palynologic samples studied from the Lagarcito Formation come from well exposed shales from the La Yesera Sur section on the eastern side of the Sierra de Guayaguás, San Juan province (Fig. 1). The psamopelitic-evaporitic sequence has gypsum and anhydrite intercalations and yields abundant conchostracans and ostracods, together with a rich palynoflora of continental (fluvio-lacustrine) origin. Preliminary palynologic studies (Prámparo and Milana, 1999; Prámparo *et al.*, 2004, 2005) indicated a palynoflora dominated in all the assemblages by gymnospermous elements mainly represented by plicate and rimulate grains. Within the plicates different species of *Cycadopites* and a rich variety of *Ephedra*-like pollen are the most frequent elements. Trilete spores are well represented by several species. A detailed study of thirteen species of verrucate trilete spores was published recently (Mego and Prámparo, 2013). Among the taxa, *Reyrea polymorphus* Herengreen, mentioned for the first time in Argentina in the Lagarcito Formation, is an excellent marker for the Aptian-Albian of northern Gondwana (Herengreen, 1973; Maghmod *et al.*, 2007). The aquatic forms are represented by the genera *Scenedesmus*, *Botryococcus*, *Crucigeniella?* *Ovoidites* and *Leiosphaeridia* (Prámparo *et al.*, 2005). Several lake episodes have been recognized in this section of the Sierra de Guayaguás but only three of them have yielded abundant palynomorphs and remains of fossil arthropods.

B) Vertebrates: fish and pterosaurs

Vertebrates from La Cantera Formation are only represented by actinopterygian fish. These fish are included at present in two large sets. On the one hand, there is

a group of basal actinopterygians that may reach 10 cm total length and are the most abundant fish in these lacustrine deposits (Plate 2, Figs. 1, 2). These specimens were preliminary interpreted on several occasions to have affinities with coccolepids and also



with chondrosteans (Spinuzza, 1986; López-Arbarello et al., 2002a, b; López-Arbarello, 2004; Castillo-Elías, 2011). During the last five years, much more and complete material has been collected and is currently under study by both of the authors (C-E. G. and G. G.) to clarify their taxonomy and systematic affinities. On the other hand, there is a basal neopterygian ganoid group, much smaller in size (5 cm maximum total length), which represents approximately 30% of the specimens collected from the site (Plate 2, Figs. 3, 4). These neopterygians have been preliminarily interpreted as "pholidophoriforms" (Flores, 1969) based mainly on their small size and the presence of scales and bones covered with ganoine. However, a recent revision including new material and considering cranial as well as postcranial characters, revealed that they are not pholidophoriforms (Giordano and Arratia, 2013), but a basal neopterygian group that is under current study by one of the authors (G.G.) as part of her doctoral dissertation. The fish from the La Cantera Formation are in general in a very good state of preservation, and most of them are found complete and articulated. However, there are some rare exceptions of disarticulated parts of the body preserved, and also isolated cranial bones and scales, patterns that may have interest for taphonomic purposes (Castillo-Elías et al., 2012).

The vertebrates from the Lagarcito Formation include fish and one pterosaur species. Among the fish, most of the specimens recorded belong to Semionotiformes (Plate 2, Fig. 5) and they were originally described by Bocchino (1973) as a different species. A posterior revision of the material, confirmed that *Neosemionotus puntanus*, Bocchino 1973, is the only taxon within the semionotiform specimens recovered from site (López-Arbarello and Codorniú, 2007). The fish assemblage from the Lagarcito Formation also includes another Actinopterygii taxon, belonging to Pleuropholidae (Plate 2, Fig. 6). This is a rare group of fish with a worldwide distribution, characterized by the presence of deep ganoid flank scales known from the Upper Triassic to the Lower Cretaceous of Europe and Gondwana (Brito and Gallo, 2002). Pleuropholids from the Lagarcito Formation are the first record of the group for Argentina (Succar and Giordano, 2012). These fish have a very small body, of about 4 cm total length, and only two specimens have so far been recorded in the main locality.

The pterosaur species from the Lagarcito Formation come from the mono-specific *Pterodaustro*-beds from the "Loma del Pterodaustro" site in Parque Nacional Sierra de Las Quijadas (Fig. 1). *Pterodaustro guinazui* (Bonaparte, 1970) is an unusu-

Plate 1. Palynomorphs and fossil plants. Figures 1-19: La Cantera Formation. Figure 1: *Couperisporites* cf. *C. complexus* (Couper) Pocock, MPLP 3949C:F30/0. Figure 2: *Ruffordiaspora* sp. MPLP 8267H: V33/4. Figure 3: *Ephedripites* sp. MPLP 2243a: Q31/0. Figure 4: *Ephedripites* cluster MPLP 3049c: U37/0. Figure 5: *Stellatopollis* sp. MPLP 2243g: E45/0. Figure 6: *Afropollis zonatus* Doyle, Jardiné and Doerenkamp MPLP 2245a: K44/4. Figure 7: *Afropollis operculatus* Doyle, Jardiné and Doerenkamp MPLP 2243a:V39/3. Figures 8-9: *Asteropollis asteroide* complex (Fig.8 *Stephanocolpites mastandreae* Volkheimer and Salas MPLP 3049c:N22/4. Fig.9 *Huitrinipollenites transitorius* Volkheimer and Salas MPLP 3049c:S22/2). Figure 10: *Tucanopollis* cf. *crisopolensis* MPLP 2243.G29/1. MPLP Figure 11: *Pennipollis peroreticulatus* (Brenner) Friis, Pedersen and Crane MPLP 3049e: D35/3. Figure 12: *Crucigeniella?* sp. MPLP 3059F:R41/0. Figure 13: *Tetrastrum* cf. *multiflorum* Batten and Lister MPLP 3043c: Q37/0. Figures 14-15: *Leiosphaeridia* spp. MPLP 8264D: N37/3; G32/0. Figures 16-17: isolated leaflet morphotype of "L-C-Microphyll trifoliolate" in Puebla 2009, Fig. 16: MIC- P461. Figure 17: MIC-P476. Figure 18: *Muscites* sp. MIC-P618a. Figure 19: *Thallites* sp. MIC-P611. The Lagarcito Formation. Figure 20: *Verrucosisporites rotundus* Singh MPLP 5861F: M34/4. Figure 21: *Concavissimisporites penolaensis* Dettmann MPLP 5967C:R38/4. Figure 22: *Impardecispora texensis* Srivastava MPLP 5861E: K27/4. Figure 23: *Scenedesmus* sp. cf. *S. novilunaris* He Cheng-quan et al., MPLP 5862D:H31/1. Figure 24: *Nodosisporites* sp. MPLP 5968F:N29/2. Figure 25: *Reyrea polymorpha* Herngreen MPLP 5967C:T38/1. Figure 26: *Classopollis* sp. MPLP 5862F: K31/0. Figure 27: *Scenedesmus* sp. aff. *S. acuminatus* f. *tortuosus* (Skujaj) Uhercovich MPLP 5862D: G23/4. MPLP (Mendoza, Paleopalintoteca Laboratorio de Paleopalintologia), UNSL (Universidad Nacional de San Luis). Microscope co-ordinates are indicated by England Finder. Scale bar: 16, 17, 18= 5mm; 19= 2.5 mm; 1- 15; 20-27= 10 µm.

Lámina 1. Palinomorfos y plantas fósiles. Figs. 1-19. Formación La Cantera. Fig. 1. *Couperisporites* cf. *C. complexus* (Couper) Pocock, MPLP 3949C:F30/0. Fig. 2. *Ruffordiaspora* sp. MPLP 8267H: V33/4. Fig. 3. *Ephedripites* sp. MPLP 2243a: Q31/0. Fig. 4. *Ephedripites* cluster MPLP 3049c: U37/0. Fig. 5. *Stellatopollis* sp. MPLP 2243g: E45/0. Fig. 6. *Afropollis zonatus* Doyle, Jardiné and Doerenkamp MPLP 2245a: K44/4. Fig. 7. *Afropollis operculatus* Doyle, Jardiné and Doerenkamp MPLP 2243a:V39/3. Figs. 8-9. *Asteropollis asteroides* complex (Fig. 8. *Stephanocolpites mastandreae* Volkheimer and Salas MPLP 3049c:N22/4. Fig. 9. *Huitrinipollenites transitorius* Volkheimer and Salas MPLP 3049c:S22/2). Fig. 10. *Tucanopollis* cf. *crisopolensis* MPLP 2243.G29/1. MPLP Fig. 11. *Pennipollis peroreticulatus* (Brenner) Friis, Pedersen and Crane MPLP 3049e: D35/3. Fig. 12. *Crucigeniella?* sp. MPLP 3059F:R41/0. Fig. 13. *Tetrastrum* cf. *multiflorum* Batten and Lister MPLP 3043c: Q37/0. Fig. 14-15. *Leiosphaeridia* spp. MPLP 8264D: N37/3; G32/0. Fig. 16.-17. Morfotipo de foliolo aislado "L-C-Microphyll trifoliolate" en Puebla 2009, Fig. 16. MIC- P461. Fig. 17. MIC-P476. Fig. 18. *Muscites* sp. MIC-P618a. Fig. 19. *Thallites* sp. MIC-P611. Formación Lagarcito. Fig. 20. *Verrucosisporites rotundus* Singh MPLP 5861F: M34/4. Fig. 21. *Concavissimisporites penolaensis* Dettmann MPLP 5967C:R38/4. Fig. 22. *Impardecispora texensis* Srivastava MPLP 5861E: K27/4. Fig. 23. *Scenedesmus* sp. cf. *S. novilunaris* He Cheng-quan et al., MPLP 5862D:H31/1. Fig. 24. *Nodosisporites* sp. MPLP 5968F:N29/2. Fig. 25. *Reyrea polymorpha* Herngreen MPLP 5967C:T38/1. Fig. 26. *Classopollis* sp. MPLP 5862F: K31/0. Fig. 27. *Scenedesmus* sp. aff. *S. acuminatus* f. *tortuosus* (Skujaj) Uhercovich MPLP 5862D: G23/4. MPLP (Mendoza, Paleopalintoteca Laboratorio de Paleopalintologia), UNSL (Universidad Nacional de San Luis). Coordenadas del microscopio indicadas por England Finder. Escala: 16, 17, 18= 5mm; 19= 2.5 mm; 1- 15; 20-27= 10 µm.

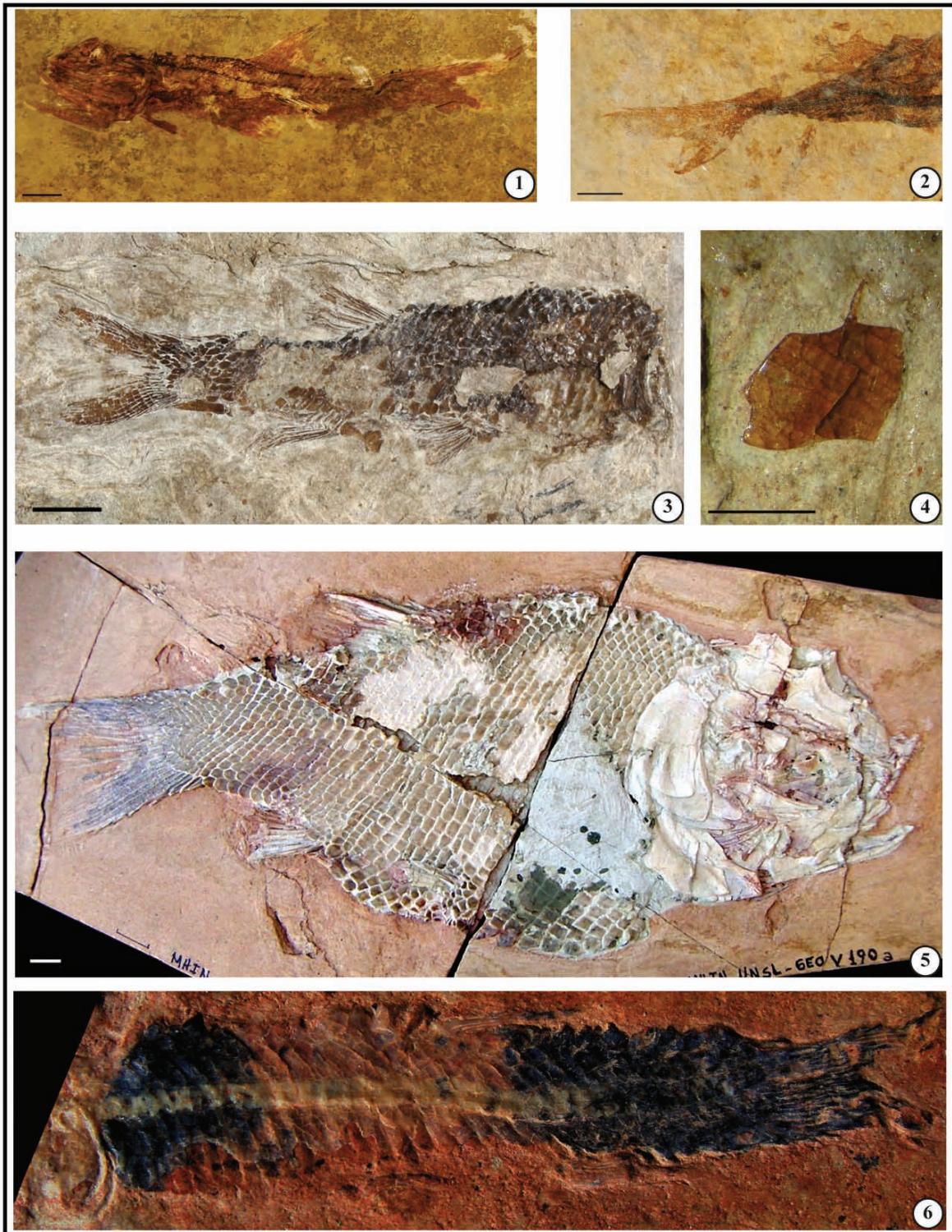


Plate 2. Vertebrates I. Figures 1-4: fish from the La Cantera Formation. 1) MIC-V 569, complete specimen of a basal Actinopterygii. 2) MIC-V 566a, a basal Actinopterygii showing its caudal peduncle and its caudal and dorsal fin. 3) MIC-V 662 post-cranial region of a Neopterygii. 4) Detail of a ganoid scale of MIC-V 631 Figures 5-6: fish from the Lagarcito Formation. 5) MIC-V 190a, *Neosemionotus puntanus*. 6) MIC-V 62, Pleuropholidae.

Lámina 2. Vertebrados I. Figs. 1-4, Peces de la Formación La Cantera 1) MIC-V 569, espécimen completo de un Actinopterygii basal. 2) MIC-V 566a, un espécimen de Actinopterygii basal mostrando pedunculo caudal y aleta dorsal y caudal. 3) MIC-V 662 region postcranial de un espécimen de Neopterygii. 4) Detalle de escama ganoidea de MIC-V 631 Figs. 5-6, Peces de la Formación Lagarcito. 5) MIC-V 190a, *Neosemionotus puntanus*. 6) MIC-V 62, Pleuropholidae. MIC (Museo Interactivo CONTACTO).

al and endemic filter-feeding pterosaur of which hundreds of specimens have been collected (Chiappe *et al.*, 1998a, b) during the last two decades from this one location. Within this large sample, there are a few complete and articulated skeletons (Plate 3), abundant partially articulated specimens (e.g. wing bones, limb bones, cervical and dorsal vertebrae, pectoral and pelvic girdles), and many isolated bones from different parts of the skeleton that can be referred to this taxon because of its particular anatomical features. The anatomy of this pterosaur is so far almost exclusively based on descriptions of the skull anatomy (Bonaparte, 1971; Sánchez, 1973; Chiappe and Chinsamy-Turan, 1996; Chiappe *et al.*, 2000, Codorníu and Paulina-Carabajal, 2013), but complete data from the postcranial skeleton is lacking. Some osteological evidence of the postcranial skeletons of *Pterodaustro* were noted from juvenile specimens (Codorníu and Chiappe, 2004), and were described especially for the cervical and caudal vertebrae (Codorníu, 2005, 2007). The lack of information does not match the availability of postcranial remains, and a detailed study on these remains is currently under preparation (Codorníu and Chiappe, in prep.). The recent discovery of geo-gastroliths in two articulated specimens of *Pterodaustro* (Plate 3), corroborate its presence, common among other archosaurs (including birds) (Wings, 2007), was so far unknown in pterosaurs until now. On the base of the largest specimens recorded it is possible to know that *Pterodaustro* was a medium to large size pterosaur. The estimation of its wingspan based on isolated bone elements (e.g., humeri, metacarpal IV, ulnae) indicate that this archosaur reached up to 3 metres (Codorníu, 2007), which largely exceeds the estimates based on previously known material that was estimated at 1.33 meters (Bonaparte, 1971; Wellnhofer, 1991). The *Pterodaustro* sample recovered from the Lagarcito Formation is unique, representing hundreds of individuals with wing spans ranging from 0.3 to 3 m, including an embryo within an egg (Codorníu *et al.*, 2004, Chiappe *et al.*, 2004). This record could certainly represent one of the rarest ontogenetic series of pterosaurs known worldwide. The numerous bones of different sizes from this site are still under morphometric and statistical study to corroborate this hypothesis with quantitative methods.

C) Arthropods

The fossil record of the La Cantera Formation shows a variety of arthropods, including insects and crustaceans (Plate 4). Flores (1969) was the first to

mention the finding of fossil insects in levels of this unit. But decades have passed after systematic studies were made (Mazzoni and Hünicken, 1984, 1987) and two families of Heteroptera Nepomorpha (water bugs) were recognized Notonectidae and Corixidae, with two new genera and species: *Canteronecta irajae* and *Romboidella popovi*. The presence of adults and juveniles of Notonectidae allowed them to also make ontogenetic interpretations (Mazzoni and Hünicken 1984) (Plate 4, Figs. 11 to 13). Sallenave (2003) reviewed the collection of insects from this geological unit housed in the University of San Luis, finding three different demic insect families (Notonectidae, Corixidae and Empidoidea) included in two orders: Heteroptera and Diptera, and seven ademic families from five insect orders: Orthoptera, Coleoptera, Hemiptera, Glosselytropea and Neuroptera. Petrulevicius *et al.*, (2005, 2010) analyzed the paleoecology of the insect association, described the new genus and species *Notonecta mazzoniae* and also recorded the presence of the oldest member of the Anisopinae subfamily, the only record for the Notonectidae family in South America. Recently, actuotaphonomic experiments have been developed in order to understand the particular preservational modes of the insect specimens, using recent representatives of the group actually living in the area and in the same type of environment (Janello, 2012). The crustacean findings from the La Cantera Formation correspond to ostracods and conchostaca. The ostracods are large size specimens preserved as casts, in many cases associated to insect remains. The casts of the valves are isolated and occasionally united in pairs (Plate 4, Figs. 1 to 4). Sallenave (2003) identified these casts as members of the Cypridacea Family, and this is the only record for this unit. At present, new methods of systematic sampling are being developed with more precise stratigraphic controls to try to recover body specimens that will allow more detailed anatomical and taxonomic comparative studies. On the other hand, in levels of the Lagarcito Formation, further north of the type locality, in the Sierra de Guayaguas, in the section known as La Yesera Sur (see Fig.1), San Juan province, an association of palynomorphs with clorophycean algae, conchostraca and ostracods has been found (Prámparo *et al.*, 2005). In this location three species of conchostraca have been identified, two of them new: *Estheriina* aff. *E. astartoides*, *Pseudestherites rivarolai* Gallego and *Dendrostracus lagarcitoensis* Gallego (Plate 4, Figs. 8 to 10). Eleven species of ostracods belonging to seven genera have also been identified and described: *Candona*, *Lymnocypridea*, *Cypridea*, *Mongolianella*, *Petrobrasia*, *Clinocypris*, and

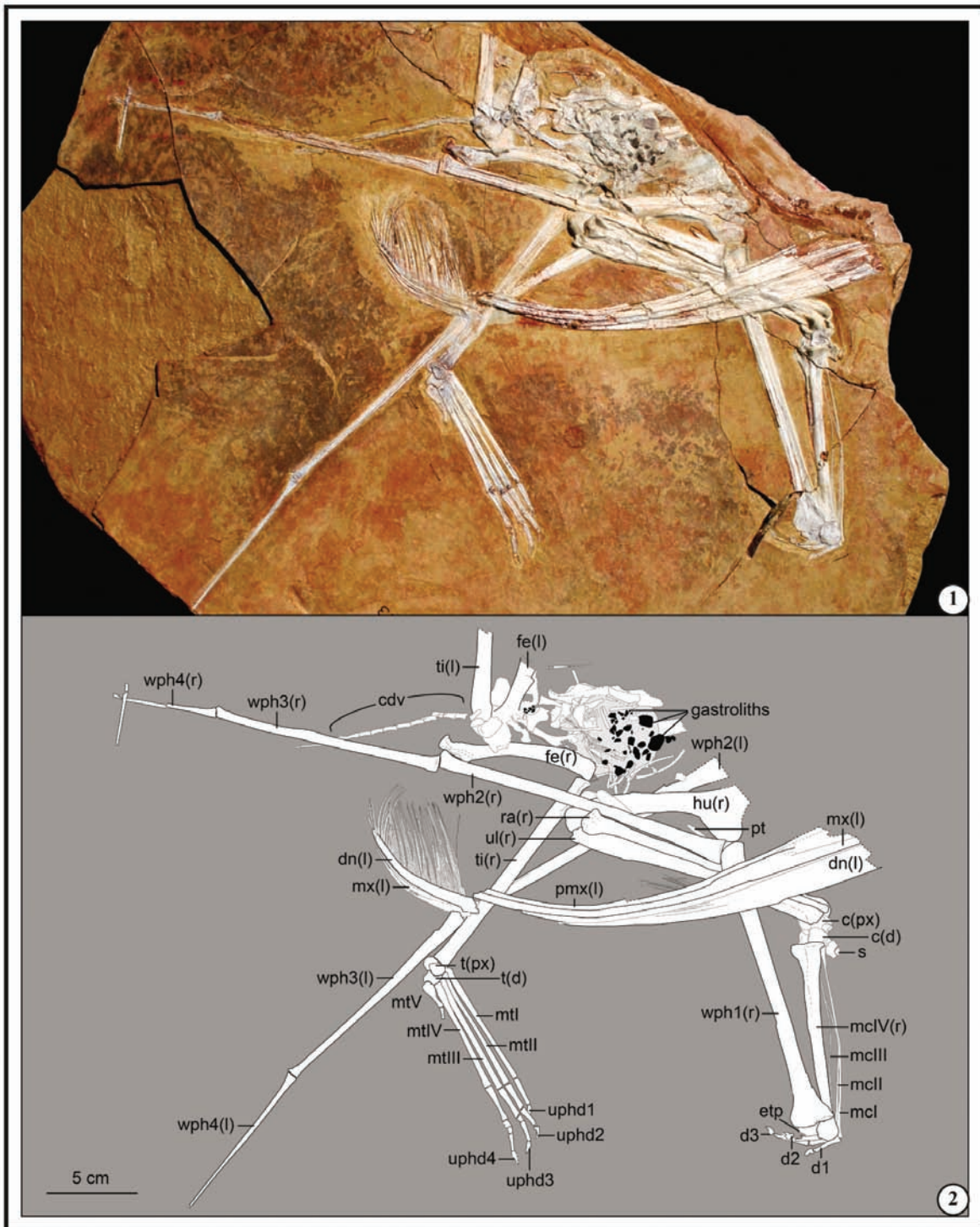


Plate 3 Vertebrates II. Photograph and interpretive drawing of *Pterodaustro guinazui* Bonaparte, MIC-V263 (Codorníu *et al.*, 2013). The preserved geo-gastroliths are denoted in black. Abbreviations: c(d), distal carpals; c(px), proximal carpals; cdv, caudal vertebrae; dn, dentary; d1-3, digits 1-3; etp, extensor tendon process; fe, femur; hu, humerus; mcl-IV, metacarpals I-IV; mtl-V, metatarsals I-V; mx, maxilla; pmx, premaxilla; ra, radius; s, sesamoid; t(d), distal tarsals; t(px), proximal tarsals; ti, tibia; ul, ulna; uphd 1-4, ungual phalanx of digits 1-4; wph1-4, phalanges 1-4 of wingfinger. (r) right; (l) left.

Lámina 3 Vertebrados II. Fotografía y dibujo interpretativo de *Pterodaustro guinazui* Bonaparte, MIC-V263 (from Codorníu *et al.*, 2013). Los geo-gastrolitos preservados están marcados en negro. Abreviaturas: c(d), carpales distales; c(px), carpales proximales; cdv, vertebra caudal; dn, dentario; d1-3, dígitos 1-3; etp, proceso extensor del tendón; fe, fémur; hu, humero; mcl-IV, metacarpales I-IV; mtl-V, metatarsales I-V; mx, maxilar; pmx, premaxilar; ra, radio; s, sesamoide; t(d), tarsales distales; t(px), tarsales proximales; ti, tibia; ul, ulna; uphd 1-4, falanges unguales de los dígitos 1-4; wph1-4, falanges 1-4 del dedo del ala. (r), derecho; (l), izquierdo.

Darwinula, included in five different families of these arthropod group (Candonidae, Ilyocypridae, Cyprididae, Pontocyprididae, Darwinulidae) (Plate 4, Figs. 5 to 7).

Results and discussion

The lacustrine sediments of the the La Cantera Formation have yielded an important paleontological association of palynomorphs, plant remains, fish, ostracods, conchostraca and insects. The fossil content of the Lagarcito Formation is made up of palynomorphs, rare plant remains, pterosaurs, fishes, ostracods and conchostraca. The studies and interpretation of the fossil content of these two lacustrine units of mid-western Argentina have revealed new and substantial information that allows a better approach to the paleoenvironmental and paleobiological reconstruction of the Aptian-Albian ecosystems in this area. It is expected that the organization of the ecosystems will resemble that of extant lentic ecosystems, which are dominated by obligate aquatic and amphibious organisms and rare or scarce facultative terrestrial organisms.

The association of fossil leaves and pollen grains found in the La Cantera Formation constitutes one of the most ancient and complete records of first angiosperms in South America (Puebla, 2009, 2010). The presence of angiosperms with very distinctive morphologies and affinities (mainly *Afropollis*) allows us to consider the studied microflora as transitional between the Northern Gondwana and Southern Gondwana Cretaceous palynofloral provinces, and assign the La Cantera Formation to the Late Aptian (Prámparo, 1990). The lack of tricolpate pollen grains in the microflora is also remarkable, and Prámparo (1994, 2012) proposed the *Stephanocolpites-Huitrinipollenites-Afropollis* Assemblage for the La Cantera Formation. The macrofossil records of bryophytes from the Early Cretaceous are scarce worldwide, and even more unusual are the findings of micro- and macro remains in the same deposit. Therefore, the bryophytes association of the San Luis Basin constitutes one the most complete records of bryophytes in Argentina (Puebla *et al.*, 2012). The occurrence of spores and macro remains of hepaticae and mosses in the same sediments suggests the *in situ* development of this group of plants. These plants grew in this part of the San Luis Basin during the Aptian under local wet conditions related to a fresh water body, in a region with seasonal semiarid conditions, where abundant polyplicate and *Classopollis* pollen grains and scarce Pteridophytes and

Bryophytes were dominant. Because the fish are the only vertebrates recorded so far from La Cantera Formation, their biological importance and the complexity of their anatomy still need more detailed anatomical and systematic revision. The review of the anatomy and the phylogenetic status of the ex "foldiform" specimens are being analyzed currently in a doctoral dissertation (Giordano and Arratia, 2013). As far as the arthropod fossils from La Cantera Formation are concerned, three endemic species of aquatic insects have been described from Notonectidae and Corixidae Families, and are unique records for the Early Cretaceous of South America. The oldest member of the Anisopinae subfamily has also been recorded, the only record for this group of Notonectidae in South America (Petrulevicius *et al.*, 2010). The endemic insects found in the sediments of the La Cantera paleolake are present in high abundance but in low density, which may indicate that the lake ecosystem corresponds to a stressed environment (Sallenave, 2003). The presence of certain features of the insect specimens, such as the transparency of the integument, the partially preserved head, and the absence of intersegmentary areas in the expanded abdomen allow us to confirm that the majority of the fossils of Notonectidae from the La Cantera Formation are exuviae or old integument and not original body fossils (Jannello, 2012). In the same study the taphonomic factor bias of the record of adult and juvenile insects from the original lake distribution is concluded. The actuotaphonomic experiment recently performed corroborates that the difference of flotability between actual insect bodies and their exuviae tends to separate them thus being deposited in different places of the lake (Jannello, 2012). The palynomorph association of the Lagarcito Formation in the Sierra de Guayaguas points to a shallow lacustrine environment. This environment was initially rich in nutrients and had high levels of evaporation, as shown by the presence of interstratified gypsum towards the top of each lacustrine episode. This gypsum is an indication of rapid environmental change, which drastically reduced the size of the water body (Prámparo *et al.*, 2005). The ostracod material from the same section includes badly preserved valves preventing a more precise taxonomic assignation. The scarce amount of ostracod articulated valves indicates mass mortality events. The fish specimens from the Lagarcito Formation include semio-notiforms, as well as pleuropholids, the same association also present in Africa in geological units of the same age (Succar and Giordano, 2012). They appear in a very good state of preservation and almost all of them are articulated. More detailed studies must be performed in order to

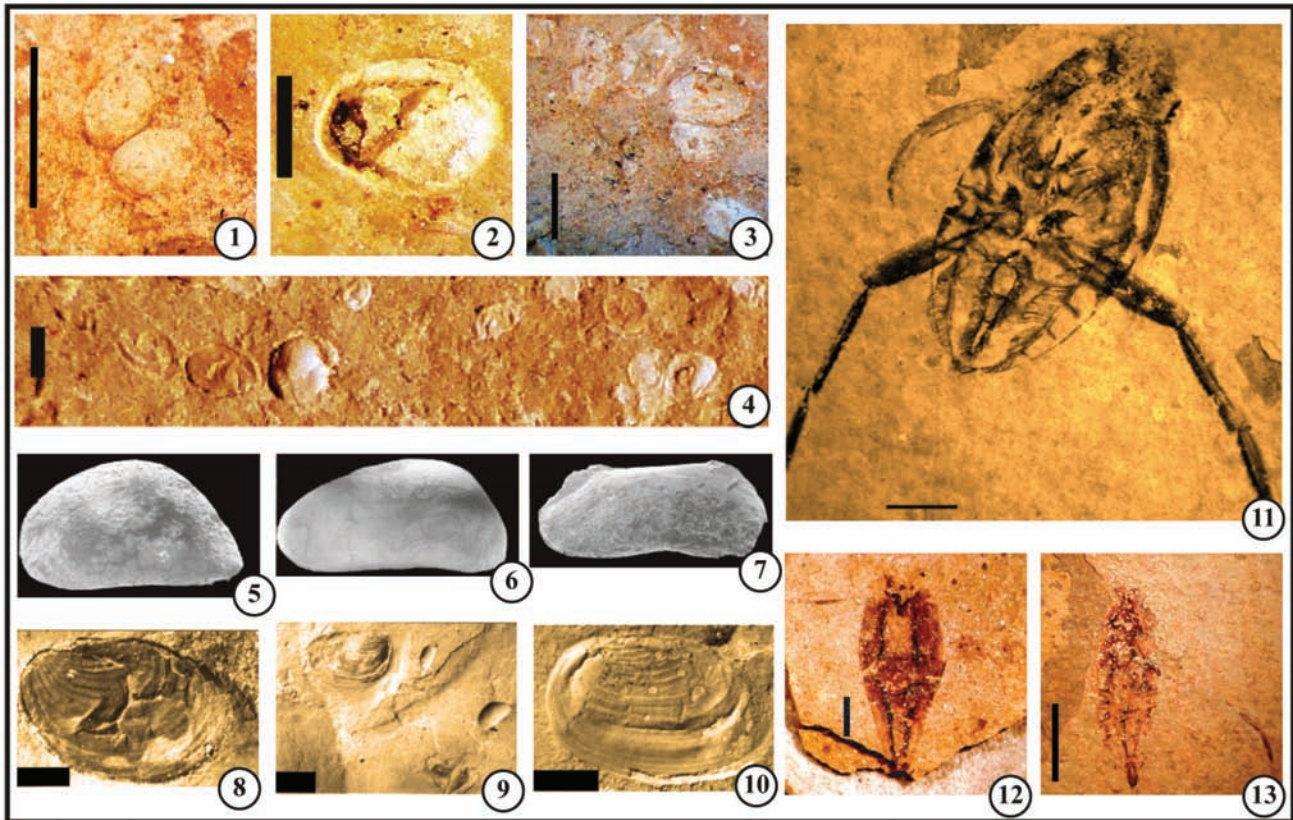


Plate 4. Arthropod macrofossils and microfossils. Figures 1-4: Ostracod casts from the La Cantera Formation. Scale bar: 1 mm. Figures 5-7: Ostracods from the Lagarcito Formation (modified from Prámparo *et al.*, 2005). Figures 5-6: *Candona* sp. A. View 75 x. Figure 7: *Limnocypridea?* sp. View: 100 x. Figures 8-10: Conchostracans from the Lagarcito Formation (Prámparo *et al.*, 2005). Figure 8: Holotype of *Dendrostracus lagarcitoensis* Gallego (Prámparo *et al.*, 2005). Scale bar: 2 mm. Figure 9: Paratype of *Dendrostracus lagarcitoensis* Gallego (Prámparo *et al.*, 2005). Scale bar: 1 mm. Figure 10: Holotype of *Pseudestherites rivarolai* Gallego sp. nov. Scale bar: 1 mm. Figures 11-13: Notodectidae from the La Cantera Formation. Figure 11: Holotype of *Notonecta mazoniae* (Petrulevicius *et al.*, 2010) Scale bar: 3 mm. Figures 12-13: Notonectidae (Jannello, 2012). Figure 12: Scale bar: 1 mm. Figure 13: Scale bar: 8 mm.

Lámina 4. Macro y microfósiles de artrópodos. Figs. 1-4: Moldes de Ostrácodos de la Formación La Cantera. Escala: 1 mm. Figs. 5-7: Ostrácodos de la Formación Lagarcito (modificado de Prámparo, *et al* 2005). Figs. 5-6: *Candona* sp. A. Vista 75 x. Fig. 7: *Limnocypridea?* sp. Vista 100 x. Figs. 8-10: Conchostracos de la Formación Lagarcito (de Prámparo, *et al* 2005). Fig. 8: Holotipo de *Dendrostracus lagarcitoensis* Gallego (en Prámparo *et al.*, 2005). Escala: 2 mm. Fig. 9: Paratipo de *Dendrostracus lagarcitoensis* Gallego (en Prámparo *et al.*, 2005). Escala: 1 mm. Fig. 10: Holotipo de *Pseudestherites rivarolai* Gallego sp. nov. Escala: 1 mm. Figs. 11-13: Notodectidae de la Formación La Cantera. Fig. 11: Holotipo de *Notonecta mazoniae* (tomado de Petrulevicius *et al.*, 2010) Escala: 3 mm. Figs. 12-13: Notonectidae (de Jannello, 2012). Fig. 12: Escala: 1 mm. Fig. 13: Escala: 8 mm.

clarify the paleobiogeographic implication of this association.

As far as the the tetrapod records in this basin are concerned, they are still limited to flying reptiles, and no other kind of archosaurs or other amniotes have yet been recovered. The evidence on the life history parameters of pterosaurs, such as growth and ontogenetic development is globally scarce. Hundreds of specimens (most belonging to different-sized isolated bones) make *Pterodaustro* one of the best represented pterosaurs worldwide. This taxon is unique in that it is represented by a wide range of different-sized individuals, allowing a comprehensive assessment of bone microstructure of a single pterosaur species

(Chinsamy-Turan *et al.*, 2008, 2009) A highly relevant paleobiological feature derived from these studies is the discovery of what seems to be medullar bone tissue within the medullar cavity of a large femur of *Pterodaustro*. This suggests that like birds and theropod dinosaurs, which also have characteristically thin bone walls, reproductively active female pterosaurs deposited a special bone tissue that is reabsorbed during the egg-laying period in which there is an intense demand for calcium (Chinsamy *et al.*, 2009). The analysis of the bone histology of the ontogenetic series of *Pterodaustro* supports the earlier hypothesis that small Jurassic pterodactyls took several years to reach adult body size (Bennett, 1995). Furthermore,

the large number of specimens available for *Pterodaustro guinazui* allows the development of a broader analysis, assessing the major histological characteristics of multiple skeletal elements from single skeletons, as well as a variety of bones from different individuals of multiple bones (Chinsamy *et al.*, 2009). The first comprehensive osteohistological assessment of multiple skeletal elements representing a range of ontogenetic sizes of a single pterosaur species was recently presented by Chinsamy *et al.*, (2008). This analysis of bone microstructure gives an insight on the developmental patterns that was unknown in pterosaurs, and shows that upon hatching, *Pterodaustro* juveniles grew rapidly for about 2 years until they reached approximately 53% of their mature body size, whereupon they attained sexual maturity. Thereafter, growth continued for at least another 3-4 years at comparatively slower rates until larger adult body sizes were attained. The recent discovery of gastroliths in *Pterodaustro* is consistent with previous interpretations of its diet, which may have included "shelled" crustaceans, and geo-gastroliths that probably helped the processing of these items within the digestive system (Codorniu *et al.*, 2013).

The goal of the current project is to integrate the autoecological reconstructions of the fossil groups and supplement them with palaeoenvironmental reconstructions based on sedimentology. Studies in development includes research on the ecological structure of the complete association, the taphonomic attributes of each kind of organism, the possible presence of bacterial sealing and other geochemical phenomena present in other well known *Konservat Lagerstätten* worldwide (Buscalioni and Fregenal Martínez, 2010).

Conclusions

During the last decade a great deal of new important paleobiological information has emerged from the Early Cretaceous of the San Luis Basin. The association of leaves and pollen grains found in the La Cantera Formation constitutes one of the most ancient and complete records of the first angiosperms in South America. The bryophyte assemblage of the same unit constitutes one the most complete records in Argentina. Insects from five different orders have been identified in this association. Three endemic species of aquatic insects have been described from the La Cantera Formation belonging to the Notonectidae and Corixidae families, and the oldest member of the Anisopinae subfamily has also been recorded, the only record for this group in South

America. The record of *Pterodaustro guinazui* from the Lagarcito Formation is one of the few pterosaur associations recovered worldwide with evidence on the life history parameters of these archosaurs, such as growth patterns and ontogenetic development. The record of Pleuropholid fish from the Lagarcito Formation is the first of this group in Argentina and the second from South America. The reproductive structure assigned to "Magnoliophyta indet" represents one of the oldest fossil records of this angiosperm features. Several new species of conchostraca and ostracoda are recorded in these levels and they are good environmental markers. Despite the amount of paleontological information that is now available from the San Luis Basin, much work remains to be done on its geology and sedimentology, and also on the taxonomy and phylogeny of the different fossil groups recovered from these cretaceous lacustrine units of the San Luis Basin.

Acknowledgements

The work included in this paper has been supported, among others, by the following grants: Agencia Nacional de Promoción Científica y Tecnológica (PICTs 1815-2008), Consejo Nacional de Investigaciones Científicas y Técnicas (PIP 0713/9), and the Universidad Nacional de San Luis (CyT N° 340103). We thank Federico Gianechini and Maria Antonia Fregenal-Martínez for the review of an earlier version of the manuscript.

Appendix

(List of taxa mentioned in the text)

Pollen and spores

Aequitriradites cf. *verrucosus* (Cookson and Dettmann) Cookson and Dettmann, 1961; *Afropollis zonatus* Doyle, Jardiné and Doerenkamp; *Afropollis operculatus* Doyle, Jardiné and Doerenkamp; *Asteropollis asteroides* complex; *Classopollis* sp.; *Concavissimisporites penolaensis* Dettmann, 1963; *Coptospora* sp.; *Couperisporites* cf. *C. complexus* (Couper) Pocock, 1962; *Crybelosporites* sp.; *Ephedripites* sp.; *Foraminisporis asymmetricus* (Cookson and Dettmann) Dettmann, 1963; *Huitrinipollenites transitorius* Volkheimer and Salas, 1975; *Impardecispora texensis* Srivastava, 1975; *Nodosisporites* sp.; *Pennipollis peroreticulatus* (Brenner) Friis, Pedersen and Crane, 2000; *Ruffordiaspora* sp.; *Reyrea polymorpha* Herengreen,

1973; *Stellatopollis* sp.; *Stephanocolpites mastandreai* Volkheimer and Salas, 1975; *Tucanopollis* cf. *cri-sopolensis* (Regali et al.) Regali and Viana, 1989; *Verrucosisporites rotundus* Singh, 1964; *Zlavisporis reticulatus* (Pocock) Pacltová and Simoncsics, 1970

Algae

Crucigeniella? sp.; *Leiosphaeridia* sp.; *Scenedesmus* sp. aff. *S. acuminatus* f. *tortuosus* (Skuja) Uhercovich, 1966; *Scenedesmus* sp. cf. *S. novilunaris* He Chengquan, Gao Rui-qi and Qiao Xiu-yun, 1992; *Tetrastrum* cf. *multiflorum* Batten and Lister, 1988

Plant macrofossils

"LC Microphyll trifoliate" in Puebla, 2009; *Muscites* sp.; *Thallites* sp.

Vertebrates

Neosemionotus puntanus Bochino; Pleurofolidae indet.; *Pterodaustro guinazui* Bonaparte

Arthropod macrofossils

Canteronecta irajae Mazzoni and Hunicken; *Romboidella popovi* Mazzoni and Hunicken, 1984
Notonecta mazzoniae Petrulevicius, Nell and Sallenave 2010

Arthropod microfossils

Conchostraca
Estherina aff. *E. astartoides* Jones 1897;
Pseudoestherites rivarolai Gallego
Ostracoda
Cypridae indet.; *Candona* sp. A and B. Braid;
Limnocypridea sp. Ljubimova; *Cypridea* sp. Bosquet;
Mongolianella sp. Mandelstam; *Petrobrasia* sp. Krömmelbein; *Clinocypris* sp. A and B Mandelstam;
Darwinula sp. Brandy and Robertson.

References

Archangel'sky, S., Barreda, V., Passalia, M.G., Gandolfo, M.A., Prámparo, M.B., Romero, E.J., Cuneo, R., Zamuner, A., Iglesias, A., Llorens, M., Puebla, G.G.,

Quattrocchio, M. and Volkheimer, W. 2009. Early Angiosperm diversification: Evidence from southern south América. *The Cretaceous Research*, 30, 1073-1082.
Arcucci, A., Puebla, G.G., Codorniú, L., Giordano, G.P. and Prámparo, M.B. 2009. A lacustrine biotic assemblage in the early Cretaceous of Central Argentina: La Cantera Formation. *10th Mesozoic Terrestrial Ecosystems and Biota* (Teruel, España, 17-19 de septiembre), *Abstract*, 111-112.
Batten, D.J., Lister, J.K. 1988. Early Cretaceous dinoflagellate cysts and chlorococcalean algae from freshwater and low salinity palynofacies in the English Wealden. *Cretaceous Research*, 9: 337-367.
Bennett, C. 1995. A statistical study of *Ramphorhynchus* from the Solnhofen Limestone of Germany - year - classes of a single large species. *Journal of Paleontology*, 69, 569-580.
Bocchino, A. 1973. Semionotidae (Pisces, Holostei, Semionotiformes) de la Formación Lagarcito (Jurásico superior ?), San Luis, Argentina. *Ameghiniana* 10, 254-268.
Bonaparte, J. F. 1970. *Pterodaustro guinazui* gen. et. sp. nov. Pterosaurio de la Formación Lagarcito, Provincia de San Luis, Argentina y su significado en la geología regional (Pterodactylidae). *Acta Geológica Lilloana*, 10, 207-226.
Bonaparte, J. F. 1971. Descripción del cráneo y mandíbulas de *Pterodaustro guinazui*, (Pterodactyloidea-Pterodaustriidae nov.) de la Formación Lagarcito, San Luis, Argentina. *Publicaciones del Museo Municipal de Ciencias Naturales de Mar del Plata*, 1, 263-272.
Brito, P. M., and Gallo, V. 2002. A new pleuropholid, *Gondwanapleuropholis longimaxillaris* ng, n. sp. (Actinopterygii: Teleostei) from the Jurassic of north east Brazil. *Comptes Rendus Palevol*, 1(8), 697-703.
Buscalioni A. and M.A. Fregenal Martínez. 2010. A holistic approach to the paleoecology of las Hoyas Konservat-Lagerstätte (La Huerguina Formation, Lower Cretaceous, Iberian Ranges, Spain). *Journal of Iberian Geology*, 36 (2): 297-326.
Castillo-Eliás, G. 2011. Osteología craneana de peces Chondrostei y análisis paleoambiental de la Formación La Cantera en su sección tipo de Sierra del Gigante, Cretácico Temprano, San Luis. Trabajo final de Licenciatura en Ciencias Geológicas, Universidad Nacional de San Luis. pp: 1-124 (inédito).
Castillo-Eliás, G., Giordano G., Codorniú L. y Arcucci A. 2012. Aspectos tafonómicos preliminares de la diversidad ictiológica en la Formación La Cantera (Aptiano Tardío, Cretácico Inferior), San Luis. XXVI Jornadas Argentinas de Paleontología de Vertebrados. Acta de resúmenes. *Ameghiniana*, 49(4), 26R.
Chiappe, L.M. and Chinsamy-Turan, A. 1996. *Pterodaustro's* true teeth. *Nature*, 379, 211-212.
Chiappe, L.M., Rivarola, D.L. Cione, Fregenal, M., Sozzi, H., Buatois, L., Gallego, O., Laza, J.H. Romero, E., López-Arbarello, A., Buscalioni, A., Marsicano, C., Adamonis, S., Ortega, P., Mc Gehee, S. and Di Iorio, O. 1998a. Biotic association and paleoenvironmental reconstruction of the "Loma del Pterodaustro" fossil site (Lagarcito

- Formation, Early Cretaceous, San Luis, Argentina). *Geobios*, 31, 349–369.
- Chiappe, L. M., Rivarola, D., Romero, E., Dávila, S. and Codorníu, L. 1998b. Recent advances in the paleontology of the Lower Cretaceous Lagarcito Formation (Parque Nacional Sierra de Las Quijadas, San Luis; Argentina). *New Mexico Museum Natural History Science Bulletin*, 14, 187–192.
- Chiappe, L. M., Kellner, W.A.W, Rivarola, D., Dávila, S. and Fox, M. 2000. Cranial morphology of *Pterodaustro guinazui* (Pterosauria: Pterodactyloidea) from the Lower Cretaceous of Argentina. *Contributions in Science Natural History Museum of Los Angeles County*, 483, 1–19.
- Chiappe, L.M., Codorníu, L., Grellet-Tinner, G. and Rivarola, D. 2004. Argentinian unhatched pterosaur fossil. *Nature*, 432, 571–572.
- Chinsamy-Turan, A., Codorníu, L., and Chiappe, L.M. 2008. Developmental growth patterns of the filter-feeder pterosaur, *Pterodaustro guinazui*. *Biology Letters*. doi: 10.1098/rsbl.2008.0004.
- Chinsamy-Turan, A., Codorníu, L., and Chiappe, L.M. 2009. Palaeobiological Implications of the Bone Histology of *Pterodaustro guinazui*. *Anatomical Record*, 292, 1462–1477.
- Codorníu, L. and Chiappe, L.M. 2004. Early juvenile pterosaurs (Pterodactyloidea: *Pterodaustro guinazui*) from the Lower Cretaceous of central Argentina. *Canadian Journal Earth Science*, 41, 9–18.
- Codorníu, L., Chiappe, L. M. and Rivarola, D. 2004. Primer reporte de un embrión de pterosaurio (Cretácico inferior, San Luis, Argentina). *Ameghiniana*, 41(4), 40R.
- Codorníu, L. 2005. Morfología caudal de *Pterodaustro guinazui* (Pterosauria: Ctenochasmatidae) del Cretácico de Argentina. *Ameghiniana*, 42, 505–509.
- Codorníu, L. 2007. Evidencias de cambios alométricos en las cervicales de *Pterodaustro guinazui* (Pterosauria, Pterodactyloidea). *Ameghiniana*, 44, 10R.
- Codorníu, L., Chiappe, L.M. and Cid, F. 2013. First occurrence of stomach stones in pterosaurs. *Journal of Vertebrate Paleontology*, 33(3), 647–654.
- Codorníu, L. and Paulina-Carabajal, A. 2013. Braincase anatomy of *Pterodaustro guinazui*. Short communications / International Symposium on Pterosaurs, Rio Ptero 2013, *Universidade Federal do Rio de Janeiro, Museu Nacional, Série Livros*, 50, 51–54.
- Cookson, I. C. and Dettmann, M. E. 1961. Reappraisal of the Mesozoic microspore genus *Aequitriradites*. *Palaeontology* 4: 425–427.
- Dettmann, M. E. 1963. Upper Mesozoic microfloras from South-Eastern Australia. *Proceedings of the Royal Society of Victoria* 77: 1–148.
- Flores, M. 1969. El Bolsón de Las Salinas en la Provincia de San Luis. Actas de las Cuartas Jornadas Geológicas Argentinas. Tomo I, P: 311–327. Mendoza.
- Flores, M. and Criado Roque, P. 1972. Cuenca de San Luis. Primer Simposio de Geología Regional Argentina. Academia Nacional de Ciencias Córdoba. 567–580.
- Friis, E.M., Pedersen, K.R., Crane, P.R. 2000. Fossil floral structures of a basal angiosperm with monocolpate, reticulate-acolumellate pollen from the Early Cretaceous of Portugal. *Grana* 39: 226–239.
- Giordano, G. and Arratia, G. 2013. Los peces ganoideos de la Formación La Cantera (Aptiano), San Luis, Argentina ¿por qué no son “Pholidophoriformes”? *Ameghiniana*, complemento de resúmenes, 50 (4), 19 R.
- Herngreen, G.F.W. 1973. Palynology of Albian-Cenomanian strata of Borehole 1-QS-1-MA, State of Maranhão, Brazil. *Pollen et Spores*, 15:515–555.
- He Cheng-Quan, Gao Rui-Qui and Qiao Xiu-Yun 1992. New Albian microphytoplankton from the Songliao Basin, northeast China. *Acta Micropalaeontologica Sinica* 9: 183–196 (in Chinese with abstract in English).
- Janello, M. 2012. Los insectos del paleolago de la Formación La Cantera (Cretácico Temprano, Sierra del Gigante, San Luis, Argentina). Trabajo Final Licenciatura en Cs. Biológicas. Biblioteca UNSL. 82 pp.
- López-Arbarello, A. 2004. The record of Mesozoic fishes from Gondwana (excluding India and Madagascar). *Mesozoic Fishes 3 Systematic, paleoenvironments and biodiversity*. Arratia G. and Tintori A. (eds.), Verlag Dr. Friedrich Pfeil., Alemania, 597–624 pp.
- López-Arbarello, A., Arratia, G. and Codorníu, L. 2002a. Cocculepids from South America and the early history of chondrostei. *Journal of Vertebrate Paleontology*, 80–81 (Abstract).
- López-Arbarello, A., Codorníu, L., Arcucci, A. and Rivarola, D. 2002b. Diversidad ictiológica en la Formación La Cantera (Cretácico Temprano) San Luis, Argentina. *Ameghiniana*, supl., 39, 13–14.
- López-Arbarello, A. and Codorníu, L. 2007. Semionotids (Neopterygii, Semionotiformes) from the Lower Cretaceous Lagarcito Formation, San Luis Province, Argentina. *Journal of Vertebrate Paleontology*, 27(4), 811–826.
- Maghמוד, M.S.; Soliman, H.A. and Deaf, A.S. 2007. Early Cretaceous (Aptian–Albian) palynology of the Kabrit-1 borehole, onshore Northern Gulf of Suez, Egypt. *Revista Española de Micropaleontología*, 39:169–187.
- Mazzoni, A. and Hunicken, M. 1984. Ontogenia de los Notonectidos (Insecta, Heteroptera) del Cretácico Inferior de San Luis, Argentina. Memoria III Congreso Latinoamericano de Paleontología, 388–393.
- Mazzoni, A. and Hunicken, M. 1987. Corixidae. (Insecta, Heteroptera) en el Cretácico Inferior de la Sierra del Gigante, San Luis, Argentina. IV Congreso Latinoamericano de Paleontología. (Bolivia) 2, 731–738.
- Mego, N. and Prámparo, M.B. 2013. Esporas triletes verrucosas de la Formación Lagarcito (Albiano?) Sierra de Guayaguas, Provincia de San Juan, Argentina. Análisis bioestratigráfico. *Revista Brasileira de Paleontología*, 16, 427–440.
- Narváez, P., Mego, N. and Prámparo M.B. 2013. Cretaceous cicatricose spores from north and central-western Argentina. Taxonomic and biostratigraphic discussion. *Palynology*, 38, 202–217.
- Pacltová, B., Simoncsics, P. 1970. New types of spores (genera and species) from the Bohemian Miocene. *Paläontologische Abhandlungen B (Paläobotanik)* 3: 599–617.

- Petrulevicius J. F, Sallenave, S. and Nel, A. 2005. Ambush predator guild of Backswimmers in the Cretaceous of Argentina. Abstracts volume: 29. III International Congress on Palaeoentomology, II International Meeting on Palearthropodology y III International Congress on amber (Fossils X3). South African National Biodiversity Institute. Pretoria, África del Sur. 7-11 de febrero.
- Petrulevicius, J.F., Nel, A. and Sallenave, S. 2010. Recent genus *Notonecta* (Insecta: Heteroptera: Notonectidae) in the Lower Cretaceous of San Luis, Argentina: Palaeoecological implications. *Annales de la Société entomologique de France (N.S.): International Journal of Entomology*, 46:1-2.
- Pocock, S. A. J. 1962. Microfloral analysis and age determination of strata at the Jurassic-Cretaceous boundary in the Western Canada plains. *Palaeontographica Abteilung B* 111: 1-95.
- Prámparo, M. B. 1989. Las esporas de Schizaeaceae (*Cicatricosisporites* y *Appendicisporites*) del Cretácico inferior, Cuenca de San Luis, Argentina. *Revista Española de Micropaleontología*, 21, 355-372.
- Prámparo, M. B. 1990. Palynostratigraphy of the Lower Cretaceous of the San Luis Basin, Argentina. Its place in the Lower Cretaceous floral provinces pattern. *Neues Jahrbuch Geol. Palaont. Abh.*, 181, 247-258. Stuttgart.
- Prámparo, M. B. 1994. The Lower Cretaceous palynoflora of the La Cantera Formation, San Luis Basin: Its correlation with other cretaceous palynofloras of Argentina. *Cretaceous Research*, 15, 193-203.
- Prámparo, M. B. 1999a. Granos de polen de primitivas Angiospermas en el Cretácico inferior de la Cuenca de San Luis y su distribución en otras Cuencas Cretácicas de Argentina. 5º Simposio sobre o Cretáceo do Brasil y 1º Simposio sobre el Cretácico de América del Sur. *Boletim do Simposio*, 539-543.
- Prámparo, M. B. 1999b. Microfitoplancton orgánico del Cretácico inferior de la Cuenca de San Luis. Parte I: Scenedesmaeaceae y Chlorococcaceae. Asociación Paleontológica Argentina. Publicación Especial Nº 6, X Simposio Argentino de Paleobotánica y Palinología (Mendoza, Octubre 1997), 39-42.
- Prámparo, M. B. 2012. Non-marine Cretaceous palynomorph biostratigraphy of Argentina. *Journal of Stratigraphy*, 36, 212-228.
- Prámparo, M.B., and Milana, J.P. 1999. Palynological and sedimentological data from the continental Lower Cretaceous Lagarcito Formation, San Juan Province, Argentina. 7º International Symposium on Mesozoic Terrestrial Ecosystems (Buenos Aires): p.52.
- Prámparo, M.B., Milana, J.P., Ballent, S. and Gallego, O. 2004. Integrated palynologic and paleontologic studies of a lower Cretaceous fluvio-lacustrine sequence of central western Argentina. 36º Annual Meeting of the American Association of Stratigraphic Palynologist and Joint Meeting with the CAP-NAMS, Ontario Canadá (october 5-8). *Palynology*, 28, p.260.
- Prámparo, M. B., Ballent, S. C., Gallego, O.F. and Milana, J.P. 2005. Paleontología de la Formación Lagarcito (Cretácico inferior), en la provincia de San Juan, Argentina. *Ameghiniana*, 42, 93-14.
- Prámparo, M.B., Quattrocchio, M., Gandolfo, M.A., Zamaloa, M.del C. and Romero, E. 2007. Historia evolutiva de las angiospermas (Cretácico-Paleógeno) en Argentina a través de los registros paleoflorísticos. *Publicación Especial 1, Ameghiniana 50º Aniversario*, 157-172.
- Puebla G.G. 2009. A new angiosperm leaf morphotype from the early Cretaceous (Late Aptian) of the San Luis Basin, Argentina. *Ameghiniana*, 46, 557-566.
- Puebla G.G. 2010. Evolución de las comunidades vegetales basada en el estudio de la flora fósil presente en la Formación La Cantera, Cretácico Temprano, Cuenca de San Luis. Tesis Doctoral. Universidad Nacional de Cuyo (PROBIOL). 180 pp. Inédita.
- Puebla G.G., Mego, N. and Prámparo M.B. 2012. Asociación de Briofitas de la Formación La Cantera, Aptiano Tardío, Cuenca de San Luis, Argentina. *Ameghiniana* 49, 217-229.
- Regali, M.S.P. and Viana, C.F. 1989. *Sedimentos do Neojurássico-Eocretácico do Brasil: Idade e Correlação com a Escala Internacional*. Rio de Janeiro, Petrobrás, 95 p.
- Rivarola D. and L. Spalletti. 2006. Modelo de sedimentación continental para el rift cretácico de la Argentina central. Ejemplo de la Sierra de las Quijadas, San Luis, Argentina. *Revist. Asoc Geol. Arg.* 61, 1: 63-80.
- Sallenave S. 2003. Insectos fósiles de la Formación La Cantera, (Cretácico Temprano) Sierra del Gigante, San Luis, Argentina. Trabajo final de Licenciatura en Ciencias Biológicas; Facultad de Química Bioquímica y Farmacia. Universidad Nacional de San Luis. Pp: 1-68 (inédito).
- Sánchez, T. M. 1973. Redescrición del cráneo y mandíbulas de *Pterodaustro guiñazui* Bonaparte (Pterodactyloidea, Pterodaustriidae). *Ameghiniana*, 10, 313-325.
- Seilacher, A. 1990. Taphonomy of Fossil-Lagerstätten: an overview. In: D. E. G. Briggs, P. Crowther (eds.), *Paleobiology*. Blackwell Science, Oxford: 266-270.
- Singh, C. 1964. Microflora of the Lower Cretaceous Mannville Group, East-Central Alberta. *Research Council of Alberta, Bulletin* 15:1-239.
- Schmidt, C.; Astini, R.; Costa, C.; Gardini, C. and Kraemer, P. 1995. Cretaceous rifting, alluvial fan sedimentation and neogene inversion, southern Sierras Pampeanas, Argentina. In A.J. Tankard, R. Suarez S., and Welsink, Eds. *American Association of Petroleum Geologist Memoir*, 62: 341-358.
- Spinuzza, J. M. 1986. Estratigrafía y paleoictiofauna de la Formación La Cantera (Cretácico), Sierra del Gigante, Provincia de San Luis. Trabajo final de Licenciatura en Ciencias Biológicas; Facultad de Ciencias Exactas, Físicas y Naturales, Departamento de Geología, Universidad Nacional de Córdoba. pp: 1-37 (inédito).
- Srivastava, S.K. 1975. Microspores from the Fredericksburg Group (Albian) of the southern United States. *Paleobiologie Continentale*, 6:1-119.
- Succar, C. A. and Giordano, P. G. 2012. Pleuropholids (Actinopterygii) from Lagarcito Formation (Albian), Sierra de las Quijadas, San Luis, Argentina and their

- taxonomic implicances. XVI Jornadas Argentinas de Paleontología de Vertebrados. Acta de resúmenes. *Ameghiniana*, 49(4), 58R.
- Uliana, M. A., and Biddle, K. T. 1988. Mesozoic-Cenozoic paleogeographic and geodynamic evolution of southern South America. *Revista Brasileira de geociencias*, 18(2), 172-190.
- Uhercovich, G. 1966. Die *Scenedesmus*-arten Ungarns. Budapest Akademiai Kiadó, 173pp.
- Volkheimer, W. and Salas, A., 1975. Die älteste Angiospermen-Palynoflora Argentinien von der Typuslokalität der unterkretazischen Huitrín-Folge des Neuquén-Beckens. Mikrofloristische Assoziation und biostratigraphische Bedeutung. *Neues Jahrbuch Geologie Paläontologie, Monatshefte*, 424-436.
- Wellnhofer, P. 1991. The Illustrated Encyclopedia of Pterosaurs. Salamander Books Ltd., London, 192 pp.
- Wings, O. 2007. A review of gastrolith functions with implications for fossil vertebrates and a revised classification. *Acta Palaeontologica Polonica*, 52, 1-16.
- Yrigoyen, M. R. 1975. La edad Cretácica del Grupo Gigante (San Luis), su relación con cuencas circunvecinas. Acta I Congreso Geológico Argentino de Paleontología y Bioestratigrafía. Tucumán. Actas II: 9-56.

Recibido: mayo 2014

Revisado: julio 2014

Aceptado: septiembre 2014

Publicado: marzo 2015

