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First occurrence of charophyte algae from a Triassic Paleolake in Argentina and their paleoenvironmental context

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ABSTRACT

This paper presents the first record of charophytes from the Triassic sedimentary rocks of Argentina and the entire southern hemisphere. Algal remains were found in the Cerro Puntudo Formation dated as Anisian (243.8 ± 1.9 Ma). The formation is part of the Cuyana Basin, which formed as consequence of the Triassic rifting of Pangaea. The paleoenvironments represented by this succession include from bottom to top: (1) a proximal to medial alluvial fan system; (2) a distal alluvial fan deposit; (3) a braided fluvial system with small channelized bodies; (4) a distal fluvial system containing rare carbonates; and (5) a carbonate-rich lacustrine system. The lacustrine facies association corresponds mainly to carbonate microbialites with three recognized facies, namely disrupted micritic limestones (**Lmd**), stromatolitic limestones (**Ls**), and oncolitic limestones (**Lo**). The **Lo** facies is rich in oncolites formed by filamentous algae in the cortex and charophyte remains (gyrogonites) in the nucleus and is interpreted as being deposited in a carbonate-rich pond environment, perhaps sourced from springs. Filamentous algae are thought to cause the precipitation of carbonates and trigger the development of micritic coatings in the ponds. Sedimentary and paleobiologic evidence suggest minor movement of the oncolites in a ponded environment where charophytes developed. The charophyte remains found in the Cerro Puntudo Formation are gyrogonites attributed to the Porocharaceae family. All the previous records for Triassic Charophyta correspond to Laurasia in the northern hemisphere, therefore, the paleolatitudinal location of this finding allows the expansion of the paleobiogeographic distribution of the group into Gondwana.

1. Introduction

Calcified algae are an important element in paleoecologic studies of carbonate sediments to unravel past environmental conditions (Cózar et al., 2003; Zatón et al., 2005; Ottone and Mancuso, 2006). Particularly, charophyte algae can be powerful indicators in paleolimnologic multidisciplinary studies. This group is important to the fossil record because this algae calcifies its reproductive structure (nucule). The fossil record of charophytes is mainly based on these biocalcified fructifications, referred to as a gyrogonite by paleobotanists. Gyrogonites and their features are useful to reconstruct the phylogeny, taxonomy and systematics of the taxa (Feist and Grambast-Fessard, 1984; Feist and Grambast-Fessard, 1991; Martín-Closas, 2003; Souliё-Marsche, 2005).

Charophytes have been extensively documented from the Silurian until today worldwide (Musacchio, 2000; De, 2003; Feist et al., 2005a; Kubota, 2005). Paleozoic families have been studied in detail and phylogenic reconstructions have been made based on the spiralization of the gyrogonite cells or its basal plate, among other features (Feist et al., 2005b; Souliё-Marsche, 2005). In spite of that, studies on charophytes from the Triassic are scarce. They have only been found in southern Sweden (Horn af Ratzien, 1954), in the USA (Peck and Eyer, 1963; Kietzke, 1989), in Germany (Breuer, 1988), in SW Poland (Zatón et al., 2005), and Slovenia (Martín-Closas et al., 2009). They occur abundantly in China (Wang and Huang, 1978; Huang, 1983).

Regarding the record in Gondwana, charophytes belonging to the Porocharaceae family have been reported from the Permian (Guadalupian) of the Paraná Basin, Brazil (Faria and Ricardi-Branco, 2009). The intracratonic basin extended up to the NE Argentina into the Chaco–Paraná Basin (Limarino and Spalletti, 2006). Notwithstanding, no charophytes have been reported from the Argentinean part of the basin.

In Argentina, several micropaleontologic investigations have been carried out in continental sediments of the Triassic (Ottone et al., 2005; Ottone and Mancuso, 2006; Zavattieri and Prámparo, 2006). Despite this, charophytes have not been described in this sedimentary context probably because previous studies have only focused on palynologic or sedimentologic research. The techniques for the extraction

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of spores most likely eliminated all evidence of charophytes in the samples.

This paper presents the first record of charophytes from the Triassic sediments of Argentina and the entire southern hemisphere. They are present in the Cerro Puntudo Formation (Mombrú, 1973), which is part of a complete nonmarine succession in the Cuyana Basin of western Argentina. This Triassic rift basin covers 60,000 km^2 with outcrops in Mendoza and San Juan provinces. The upper section of the Cerro Puntudo Formation has been dated recently, by palynologic and U–Pb zircon (SHRIMP) data, as 243.8 ± 1.9 Ma (Mancuso et al., 2010). So far paleontologic studies of this formation have been focused on the paleoflora and trace fossils (Krapovickas et al., 2008; Mancuso, 2009). A detailed facies analyses of the Cerro Puntudo Formation is provided in this contribution to determine the paleoenvironmental context of the charophyte record. The aim of this paper is to describe the paleoecologic conditions under which the charophytes lived and provide a glimpse of the distribution of the group in Pangaea.

2. Geologic setting

Triassic sedimentary basins of Argentina formed as part of the rifting event associated with the pre-breakup of Pangaea in the SW margin of Gondwana (Uliana and Biddle, 1988). This event originated

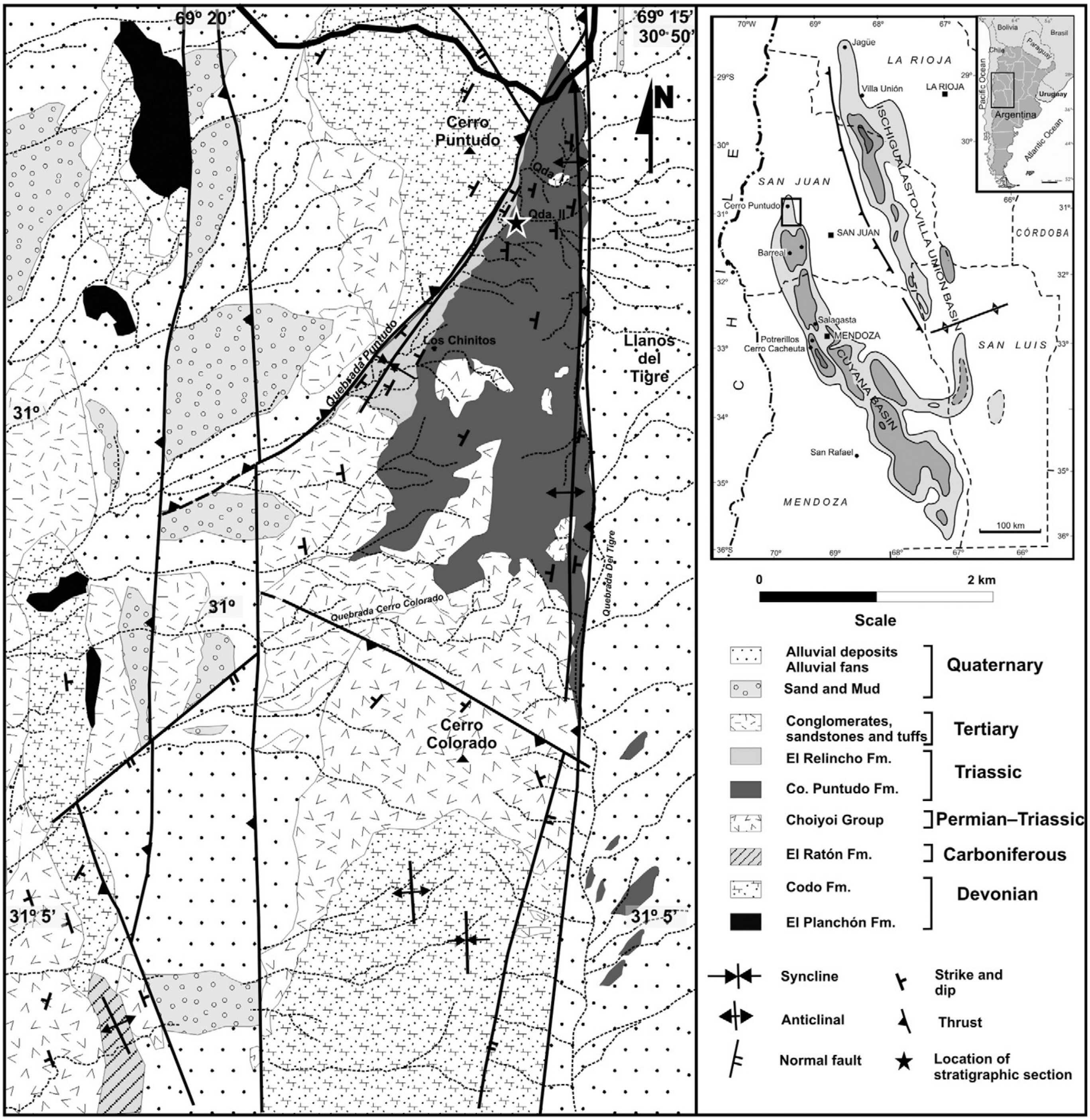


Fig. 1. A) Location map of Cuyana Basin, and geologic map of Cerro Puntudo area. Modified from Mancuso et al. (2010).

Table 1
Summary of the Cerro Puntudo Formation facies association.
Modified from Mancuso (2009) and López-Gamundí and Astini (2004).

Facies	Lithology	Structures	Bedding	Fossil content	Lateral and vertical relationships	Interpretation
CP-A (*180 m thick*)	Clast-supported, poorly sorted, rounded and subangular pebble to cobble, red to reddish brown conglomerate (**Gcm**)	Massive, matrix composed of medium- to coarse-grained sandstone	Lenses to tabular beds are, 1.8–2.3 m in thickness that extend laterally for several meters with slightly erosional basal contacts and planar upper contacts.		Gcm facies overlies Choiyoi Group and pass laterally and vertically to Sn and Sp1 facies. Gcm facies is interbedded with Gmm facies.	*Proximal to medial alluvial fan deposits*
	Moderately sorted, medium to coarse, red sandstone (**Sm**, **Sp1**)	Graded bedding, planar cross-stratification (co-sets up to 20 m thick), lag deposits	Lenticular to tabular beds from 0.5 to 1.5 m thick, persist laterally for tens of meters, with slightly erosional bases.		Sm and Sp1 facies overlie and pass laterally into Gcm.	
CP-B (*360 m thick*)	Clast-supported, poorly sorted, rounded to subangular pebble, red to reddish brown, conglomerate (**Gcp**)	Graded bedding, planar cross-stratification (co-sets up to 10 m thick), lag deposits	Lenticular to tabular beds, up to 2 m thick, persist laterally for hundreds of meters, with slightly erosional lower contacts.		Gcp facies overlie Gcm, Sm, and Sp1 facies (CP-A) and is overlain by Sm1 and Sp2 facies.	*Braided fluvial system deposits associated with distal alluvial fans*
	Moderately sorted, medium to coarse, reddish brown, sandstone (**Sm1**, **Sp2**)	Massive or planar cross-stratification	Lenticular to tabular beds, 1 m thick, persist laterally for several meters with an erosional base.	*Skolithos*	Sm1 and Sp2 facies overlie Gcp facies and are overlain by Sm2, Sp3 and St facies (CP-C)	
CP-C (*80 m thick*)	Well sorted, medium to fine, reddish brown sandstone (**Sm2**, **Sp3**, **St**)	Massive or tabular and trough cross-stratification (cosets up to 15 m thick)	Lenses of 0.5–1.5 m thick, persist laterally for 10 m, with slightly erosional basal contacts.		Sm2, Sp3, St facies overlie Fm1 facies and pass laterally and vertically to Fm1 facies. Both Sm2, Sp3, St facies and Fm1 facies are interbedded with each other.	*Fluvial system deposits associated with distal alluvial fan system and lacustrine interbeds*
	Tuffaceous, reddish brown and white siltstone (**Fm1**)	Mottling, flat lamination	Tabular beds, 0.5–0.8 m in thickness, persist laterally for hundreds of meters. Upper and lower non-erosional contacts.	Rhizoliths and *Scoyenia*	Fm1 facies overlie Sm2, Sp3, and St facies and passes laterally and vertically into Sm2, Sp3, and St facies.	
	Compact gray limestone (**Lm**)	Massive	Lenses up to 0.7 m thick and persist laterally for 30 m, with planar non-erosional upper and lower contacts.		Lm facies is interbedded with Fm1 facies.	
CP-D (*75 m thick*)	Stromatolitic limestone (**Ls**)	Stromatolitic structure (flat to domed lamination)	Tabular to lenticular beds, from 8 up to 100 cm thick. Rare mudcracks.	Microbial filaments, charophytes, ostracodes	Ll facies overlie Fm2, Fl, Sm3, Sh, Sr, Lo, Tm, and Tl facies and pass laterally and vertically into Fm2, Fl, Sm3, Sh, Sr, Lo, Tm, and Tl facies.	*Lacustrine system deposits*
	Altered/disrupted micritic limestone (**Lmd**)	Nodular and mottled fabric	Lenticular beds, from 5 to 70 cm thick.	Rhizoliths	Associated with Md, Sm3, Sh, and Sr. Laterally grading into Lo.	
	Oncolitic limestone (**Lo**)	Oncolitic microbial texture, oncolite sizes range from 0.5 to 10 cm (diameter)	Lenticular beds, from 8 to 70 cm thick.	Microbial filaments, charophytes, ostracodes	Lateral grading into Ld. Interbedded with Md	
	Reddish-purple mudrock (**Md**)	Fine horizontal lamination, soft sediment features	Tabular beds from 5 to 100 cm in thickness.	Vertical and polygonal mudcracks	Lateral grading into Ll, Ld, Lo, and Tm. Interbedded with Ll, Ld, Lo, Tm, Fm2, Fl, Sm3, Sh and Sr.	
	Calcareous, reddish-brown siltstone (**Fm2**, **Fl**)	Massive to fine flat lamination, soft sediment features	Tabular beds, 0.5–0.8 m in thickness, persist laterally for hundreds of meters with non-erosional contacts.	Plant debris and rhizoliths	Fm2 and Fl facies overlie Ll, Sm3, Sh, Sr, Lo, Tm, and Tl facies and pass laterally and vertically into Ll, Sm3, Sh, Sr, Lo, Tm, and Tl facies.	
	Well sorted, calcareous, reddish-brown sandstone (**Sm3**, **Sh**, **Sr**)	Massive, flat-lamination, to ripple cross-lamination	Tabular beds, 0.5–0.8 m in thickness persist laterally for hundreds of meters, and have non-erosional boundaries.	Rhizoliths	Sm3, Sh, and Sr facies overlie Ll, Fm2, Fl, Lo, Tm, and Tl facies and pass laterally and vertically into Ll, Lo, Tm, and Tl facies.	

Table 1 (*continued*)

Facies	Lithology	Structures	Bedding	Fossil content	Lateral and vertical relationships	Interpretation
	Light green tuff and tuffite (**Tm**, **Tl**)	Massive to thick lamination (3 cm thickness)	Tabular beds 0.5–0.8 m in thickness, persist laterally for hundreds of meters with non-erosional contacts.	Plant debris, rhizoliths, and vertebrate remains	Tm and Tl facies overlie Ll, Fm2, Fl, Sm3, Sh, Sr, and Lo facies and pass laterally and vertically into Ll, Fm2, Fl, Sm3, Sh, Sr, and Lo facies.	

several rift basins (half-grabens), including the Cuyana Basin (Stipanicic, 2001) (Fig. 1). The basin possesses large and well-exposed outcrops and it is widely known for its rich paleontologic content and potential as a hydrocarbon reservoir. The Cuyana Basin includes two half-grabens, the southern and northern sub-basins (López-Gamundí, 2010), for which the master border fault alternates with the northern fault to the east and the southern fault on the west (e.g., Ramos and Kay, 1991; Legarreta et al., 1992; Barredo, 2005). The half-grabens are filled by up to 6000 m of continental sediments, dominated by alluvial, fluvial, and lacustrine deposits (Stipanicic, 2001). A connection between the sub-basins has been recognized through lithologic similarities (Mombrú, 1973; Baldis et al., 1982) and expanded areal extensions of the depocenters (Kokogian et al., 2001). However, Stipanicic (2001) supports disconnected depocenters for each sub-basin. This is reflected in the use of a different stratigraphic nomenclature for the depocenters.

Cerro Puntudo (30°98′42″S 69°27′42″W) is the northernmost outcrop of the Cuyana Basin (Fig. 1). It is located in San Juan province, west–central Argentina. In this area, the Cerro Puntudo Formation corresponds to the first sequence in a synrift stage of the basin and it developed at the W margin of the northern half-graben of the Cuyana rift with its normal bounding fault located in the E, while in the southern half-graben, the fault is located to the W. It has been identified by López-Gamundí and Astini (2004) as the infilling of the low accommodation zone of the rift. The formation represents a unique sedimentary succession (Strelkov and Álvarez, 1984) that varies from alluvial fan to fluvio-lacustrine deposits. The paleoflora and fauna content of the Cerro Puntudo Formation is scarce. There are reports of spores with Pteridophyta and Lycophyta affinity, pollen grains with Araucariaceae affinity, and rhizoliths (Mancuso, 2009; Mancuso et al., 2010). With respect to the fauna, trace fossils are found in the more distal part of the alluvial fans, including the ichnofacies *Skolithos* and *Scoyenia* (Krapovickas et al., 2008). The *Scoyenia* ichnofacies is recognized in the lacustrine system as well. Vertebrate remains correspond to a unique fragment of pelvic girdle assigned to a possible basal archosaur (Mancuso et al., 2006).

The paleoenvironments represented by this succession include from bottom to top (Table 1) (Table 2) (Fig. 2): (1) a proximal to medial alluvial fan system (Facies CP-A); (2) a distal alluvial fan deposit; (3) a braided fluvial system (CP-B) with small channelized bodies; (4) a distal fluvial system (CP-C) containing rare carbonates; and (5) a carbonate-rich lacustrine system (CP-D). The limestone beds of CP-D facies contain mainly microbial fabric represented by a 30 m thick succession (Fig. 2) (López-Gamundí and Astini, 2004; Mancuso et al., 2010). These facies are mostly located to the NW of the Cerro Puntudo depocenter (N margin of the northern sub-basin) while siliciclastic facies in this formation are dominant to the SE. The charophyte-rich beds of CP-D facies are the focus of this paleoecologic study.

Table 2
Description of the lithofacies code used in Table 1.

Lithofacies	Description
Gcm	Conglomerate clast-supported massive
Sm	Sandstone massive
Sp1	Sandstone planar cross-stratification
Gcp	Conglomerate clast-supported planar cross-stratification
Sm1	Sandstone massive
Sp2	Sandstone planar cross-stratification
Sm2	Sandstone massive
Sp3	Sandstone planar cross-stratification
St	Sandstone trough cross-stratification
Fm1	Tuffaceous siltstone flat-lamination
Lm	Limestone massive
Ls	Limestone stromatolitic
Lmd	Limestone micritic disrupted
Lo	Limestone oncolitic
Md	Mudrock
Fm2	Calcareous siltstone massive
Fl	Calcareous siltstone flat-lamination
Sm3	Sandstone massive
Sh	Sandstone flat-lamination
Sr	Sandstone ripple cross-lamination
Tm	Tuffite massive
Tl	Tuffite lamination

3. Methodology

All seven limestone beds with an oncolitic–stromatolitic fabric found in the Cerro Puntudo Formation were sampled. Polished sections were done at the Laboratorio de Geología of the Universidad Nacional de San Luis (UNSL) for each oncolitic bed. They were described using a binocular low magnification microscope (Nikon NI-150 SMZ 1000). Thin sections were prepared at the Instituto de Geocronología y Geología Isotópica (INGEIS) of Buenos Aires. The sections were stained with Alizarin S to differentiate calcite from dolomite and were described using a petrographic microscope (Olympus BX-51) to determine the microfacies. The microfacies determination was after Dunham (1962) textural classification for fossiliferous limestones.

Samples were processed with the copper sulfate method following the technique described by Feist et al. (2005a) for extraction of calcareous microfossils at the Laboratorio de Palinología of the Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA) of Mendoza. However, the technique damaged the surface of the gyrogonites, so they were extracted manually from the rock matrix with needles under binocular low-magnification microscope. The gyrogonites were observed and photographed under a scanning electron microscope (SEM) at the Laboratorio de Microscopía Electrónica y Microanálisis (LabMEM) of the UNSL. The total gyrogonites extracted were 12 and they are housed in the Paleobotany Collection at the Museo de Ciencias Naturales y Antropológicas Juan Cornelio Moyano (MCNAM) of Mendoza City.

4. Results

Table 1 summarizes all the facies present in the Cerro Puntudo Formation. Only the beds containing oncolitic carbonate are studied in detail here. Extensive discussion of the siliciclastic facies can be found in López-Gamundí and Astini (2004) and Mancuso (2009).

4.1. Sedimentology

4.1.1. Limestone beds

Limestone beds are interbedded and grade laterally to mudstones and sandstones, and are also interbedded with volcanic rocks (Table 1, Fig. 3). Three facies are established for the limestone beds: stromatolitic limestones (**Ls**), altered/disrupted micritic limestones

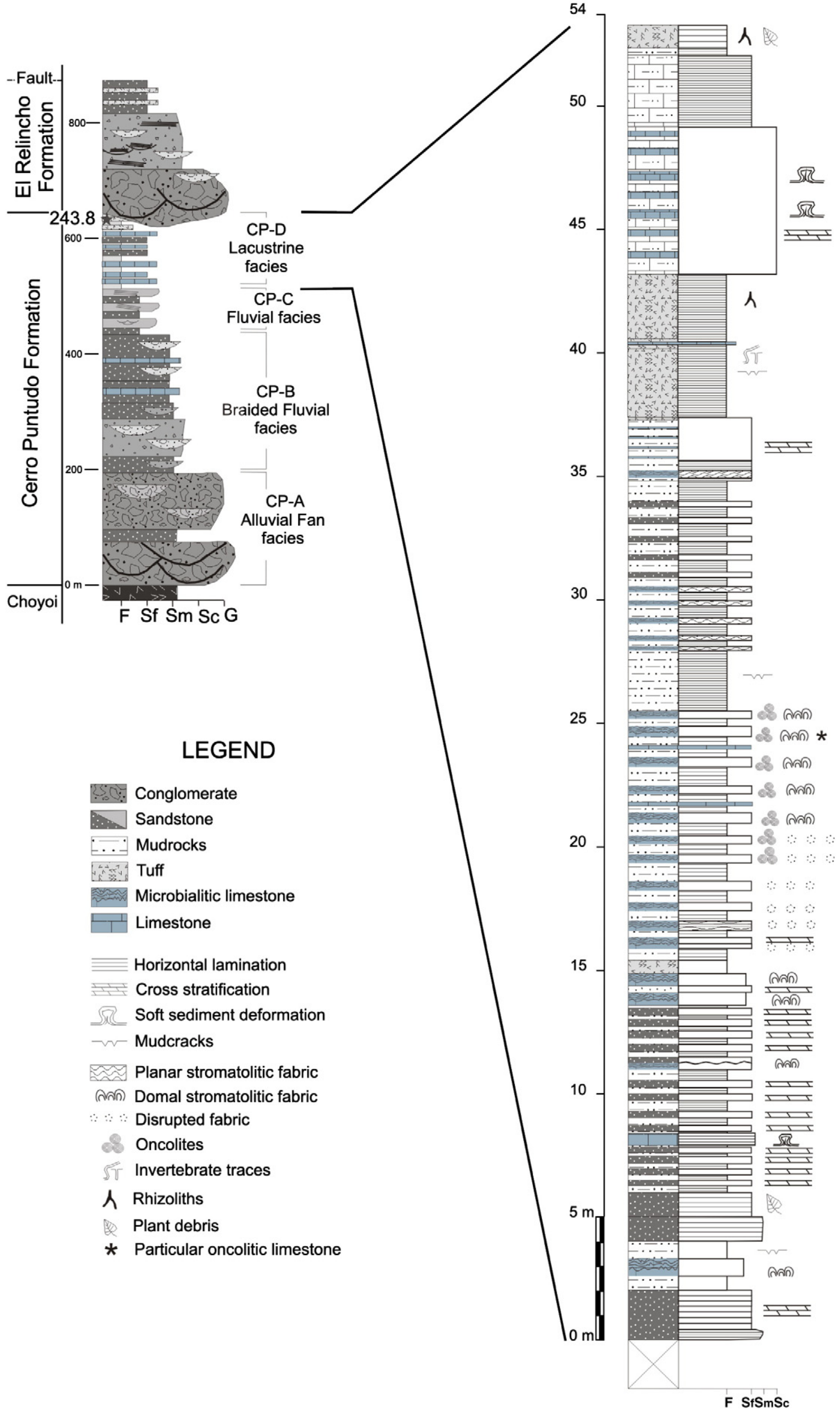


Fig. 2. General stratigraphic profile of the Cerro Puntudo Formation and specific section of the lacustrine succession at Cerro Puntudo depocenter, Cuyana Basin. See exact location of the section in Fig. 1.

Fig. 3. Cerro Puntudo outcrop view, alternation of limestones and siliciclastic facies can be seen. Section is between 8 and 26 m of the stratigraphic profile in Fig. 2.

(**Lmd**), and oncolitic limestones (**Lo**). **Ls** is represented by stromatolites with flat lamination and domal fabrics. **Lmd** is represented by beds that show pedogenic features such as fabric disruption by rhizoliths. **Lo** includes all the rich charophyte microbialites which are the main focus of this study. These beds are associated with remains of organisms, such as microbial filaments, charophyte algae, ostracodes, *Porifera spicules*, and plant stems.

4.1.2. Oncolitic limestone facies (**Lo**)

This facies is one of the most common of the carbonates found in the studied succession. The carbonate beds are light gray in color and massive with dispersed oncolites and erosive basal contacts. They vary in thickness from 8 to 68 cm thick (Fig. 4A). In the upper section of the succession, a particular stratum (marked by a star in Fig. 2) is formed by three oncolitic carbonate beds, each one with a fine layer of siliciclastic mudstone (3 cm in thickness) at the top (Fig. 4A). Oncolites in these beds are inversely graded.

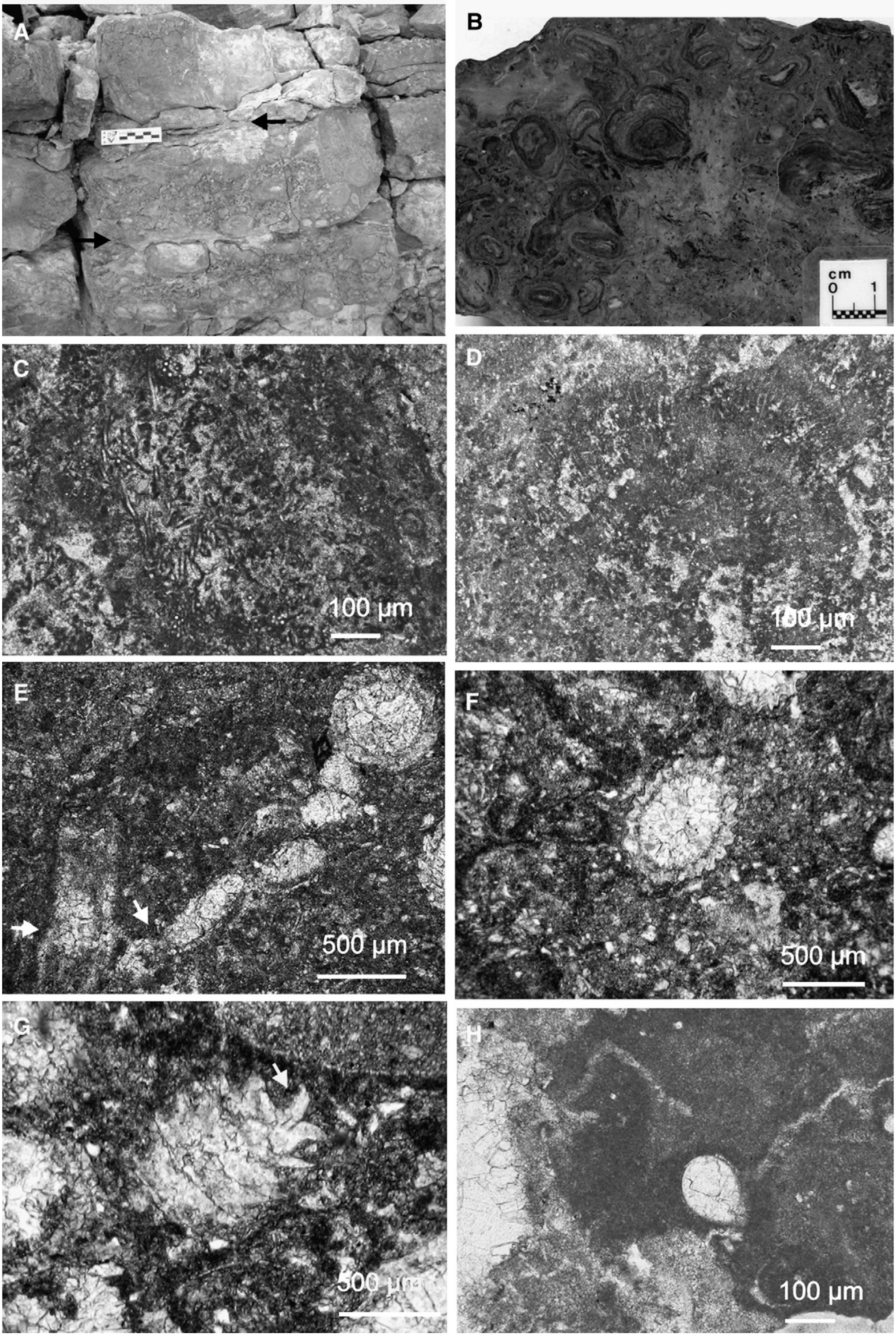
In thin section, the microfacies fabric consists of scattered coated grains in a matrix composed predominantly of primary micrite and with minor siliciclastic silt grains. Coated grains are mainly oncolites that vary in size from 1 to 12 cm in diameter with both single and composite forms (Fig. 4A, B). They have irregular margins and multiple concentric laminae in the cortex coating of one or more nuclei. Each lamina measures approximately 50 μm in thickness. Between the laminae, straight or softly curved tubules between 10 and 20 μm are present (Fig. 4C, D). The external walls of the tubules are composed of micrite. The tubules are found in small aggregates or as tangled masses (Fig. 4C). Their disposition in the cortex of the oncolites is radial (Fig. 4D).

In most of the oncolites, the nucleus consists of phytoclasts of charophytes thalli or reproductive structure (gyrogonites). Transversal sections of the thalli measure approximately 250 to 300 μm. Longitudinal sections measure 1000 to 1750 μm long and 200 to 300 μm wide. No cortical cells or corticated external features can be seen but apparent nodes are observed. The thalli remains are associated to the gyrogonites (Fig. 4E). Longitudinal sections of the gyrogonites are 600 μm long (polar axis) with an approximate diameter of 400 μm (equatorial axis) (Fig. 4F, G) and have been completely recrystallized by spar (Fig. 4E, F, G). Phytoclasts are also recrystallized by spar and can be seen in longitudinal and transverse sections with micritic coatings. In transverse section they measure approximately 0.2 to 0.6 mm wide. These gyrogonites compose more than 10% of the grains and in most cases they have thin micritic coatings. Generally these reproductive structures are disarticulated and associated with thalli (Fig. 4E). Under the SEM no special features (ornamentations) could be recognized on the surface of gyrogonites. Dispersed in the matrix, transversal sections of coated stems (phytoclasts) are present along with ostracode valves and fragments of siliceous sponge spicules. Ostracodes are recrystallized by spar and are represented by disarticulated valves that measure 200 μm (Fig. 4H).

4.1.3. Interpretation

The oncolites that characterize this facies are the result of carbonate coatings that precipitated around particles such as gyrogonites and thalli in the site of growth of the charophytes. Tubules observed in the oncolitic cortices are interpreted as filamentous microbial remains. They are thought to be responsible for the precipitation of carbonates by triggering the development of micritic coatings (Platt and Wright, 1991; Shiraishi et al., 2008). According to Freytet and Verrecchia (1998), numerous genera of cyanobacteria (e.g., *Plectonema*, *Chaetophora*, *Grongosira*) have been observed to be involved in the formation of recent oncoids. Also *Homoeothrix* filaments have been reported as the main oncoid builders from a recent lacustrine environment in Mexico (Winsborough et al., 1994). These genera are probably the best modern analogs of microbial filaments for the ones described here.

Charophytes, ostracodes, and sponges characterize typical pond environments protected from strong currents and with slow flowing waters. Particularly, the presence of charophyte algae is an indicator of approximate depths of no more than 10 m (Cohen and Thouin, 1987). Sponges indicate oxic bottom conditions. The presence of coated phytoclasts suggests that macrophytic vegetation was developed in adjacent areas. The nuclei of the coated grains developed in these settings under the described conditions. Subsequently, moderate


A
B
cm
0
1
C
100 µm
D
100 µm
E
500 µm
F
500 µm
G
500 µm
H
100 µm

energy currents and agitation may have promoted fragmentation of the material and the generation of abundant debris and phytoclasts that encrusted the oncolite cortex. These plant debris probably belonged to hygrophyte plants that were encrusted in submerged nearby environments with minor transport (Arenas et al., 2007). This carbonate encrustation process has been observed in modern shallow carbonate ponds (Alonso-Zarza, 2003).

Diagenesis altering the original fabric consists of spar recrystallization replacing bioclasts and infilling voids (Arenas et al., 2000; Arenas et al., 2007; Jones and Renaut, 2010). No subaerial exposure or pedogenic features are evident indicating subaqueous conditions. A further explanation of the interpretation of the origin of the facies is provided in the Discussion (Section 5).

4.2. Systematic paleobotany

The filamentous micritic tubules observed in thin sections are considered to be the remains of microorganisms, probably cyanobacteria (prokaryotic algae) or other filamentous algae, such as Chlorophyta (eukariotic algae). The characters observed in the microbial filaments, such as tubes 10 and 20 μm in width that are straight or softly curved and lacking ramifications (Fig. 4D), are considered diagnostic of the morphogroup of tubiform calcified algae (Riding, 1991). Based on the morphologic attributes mentioned, tubiform algae show affinities with Cyanophytes and the type of preservation observed in thin sections can be diagnostic of the associated microorganism (Freytet and Verrecchia, 1998). The charophytes of the Cerro Puntudo Formation possibly belong to the Porocharaceae family. So far, this family is the only globally known taxa for the Triassic (Feist and Grambast-Fessard, 1991). This is a consequence of the abrupt decrease in charophyte families towards the end of the Permian. During the Paleozoic, charophytes had experienced numerous extinctions counterbalanced with the rise of new families (Grambast, 1974). From the Triassic onwards the Porocharaceae family constitutes the common stock from which all the post-Paleozoic families are derived (Bilan, 1988; Riding, 1991). This family comprises two subfamilies, Porocharoidea and Stellatocharoidea. The latter includes all genera with a neck-like or conical apex (Breuer, 1988).

Unfortunately when the preservation state of gyrogonites is poor, extractive techniques turn out to be too aggressive and damage their surface (Kubota, 2005). This is the case for the Cerro Puntudo Formation gyrogonites. The characters of the base of the gyrogonites cannot be thoroughly characterized, nevertheless, a description is provided here.

Division: Charophyta (Migula, 1897)
Class: Charophyceae (Smith, 1938)
Order: Charales (Lindley, 1836)
Family: Porocharaceae (Grambast, 1962)
Subfamily: Stellatocharoideae (Grambast, 1962)
gen. et sp. indet.
Figs. 4G; 5A, B, C

Gyrogonites with spirals of constant breadth, vertically bent at the summit or straight forming a projection in the form of a neck, having a pentagonal, star-shaped or round opening (Bilan, 1988).

Material. 4 gyrogonites, corresponding to the collection numbers: MCNAM-PB 1520, 1521, 1522, and 1523.

Description. Large gyrogonites that measure 500 μm high (LPA) and 350 μm wide (LED); the resulting ISI (isopolarity index) of 122–200% determines a prolate to subprolate shape; and the ANI (anisopolarity index) of 45–57% determines an ellipsoidal shape. The presence of an apical neck is observed so the L index is provided, being 700 to 1000 μm. Spiral cells are about 50 μm high and concave. They coil the gyrogonite with at least five convolutions visible in lateral view. Their inclination angle and breadth are constant. The sutures between the spirals are visible though not prominent. The base is rounded while the apex has an apical neck of 125 to 150 μm high and 100 μm width in lateral view showing a conical shape and slightly vertically bent projections.

Subfamily: Porocharoideae (Grambast, 1961)
gen. et sp. indet.
Figs. 5D, E, F, G, H

Gyrogonites with an apical opening not lying at the top of a neck (Feist and Grambast-Fessard, 1984).

Material. 8 gyrogonites corresponding to the collection numbers: MCNAM-PB 1524, 1525, 1526, 1527, 1528, 1529, 1530, and 1531.

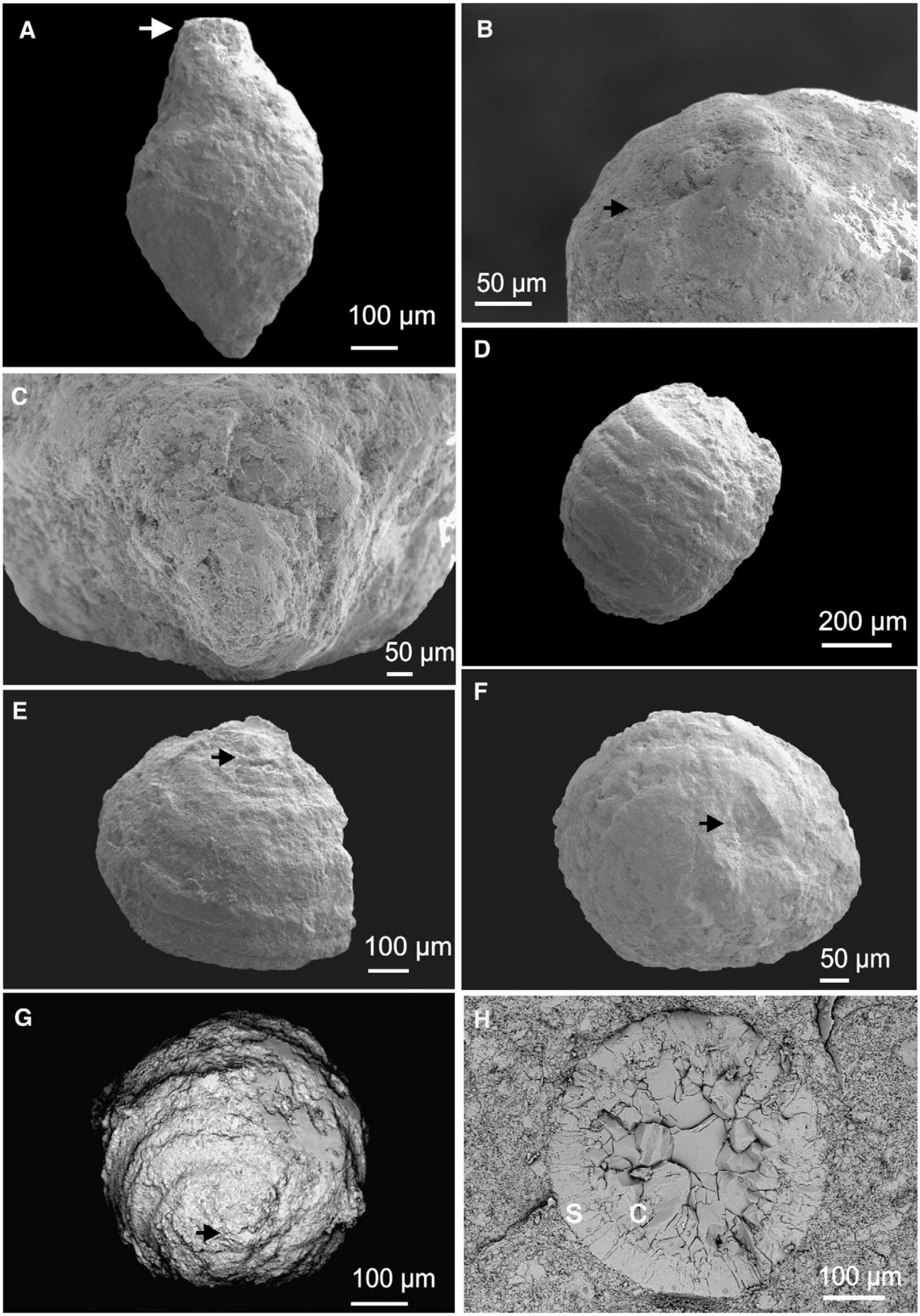
Description. The gyrogonites are smaller than the previously described. They measure 650 to 700 μm high (LPA) and 550 to 600 μm wide (LED). ISI is 116–118% determining a subprolate shape; ANI is 46–57% corresponding to an ellipsoidal to subobovoidal shape. Spiral cells visible in lateral view show approximately ten convolutions and are 100 μm wide. The apex and base are rounded with no apparent projections. Apex and base are not well preserved so the presence of a small round apical pore is doubtful.

5. Discussion

The Cuyana rift basin is similar to the tectonic structure of Lake Tanganyika (Cohen, 1990) and Lake Bogoria (Renaut and Tiercelin, 1994) (East Africa). The Cerro Puntudo Formation deposited at the N margin of the Cuyana rift in a setting similar to the platform or ramp lake margin setting defined by Cohen (1990). This area has been characterized as a low gradient area with a slow subsidence rate at a basinal hinge (Cohen, 1990). Indeed, López-Gamundí and Astini (2004) interpret the Cerro Puntudo Formation as the infilling of a zone with a relatively low accommodation rate within the rift. Lake environments in such settings commonly present low gradients (Platt and Wright, 1991) and the development of palustrine facies and pedogenic alteration (Platt and Wright, 1991; Alonso-Zarza et al., 1992; Pla-Pueyo et al., 2009; Alonso-Zarza and Wright, 2010). These characteristics provide an environmental model under which the Cerro Puntudo deposits can be interpreted.

Siliciclastic facies (CP-D) attributed to the lacustrine system of the Cerro Puntudo Formation along with paleobiologic evidence provide a sedimentologic context for the oncolitic limestone facies (**Lo**). Fm2, Fl, Sm3, Sh, Sr, Tm, and Tl facies are equivalent to the interbedded mudstones, limestones, and subordinated tuff facies of López-Gamundí and Astini (2004). They interpret them as discrete sheetflood deposits at the margins of a shallow carbonate-rich lake environment. More likely, the stratal geometry of **Lo** (lenticular morphology), its limited lateral extent (several decimeter wide), and limited thickness as well, is indicative of restricted pond settings (Gierlowski-Kordesch, 1998). Vertical and lateral relations show that **Lo** facies are interbedded and laterally interfingered with facies of CP-D association (Table 1). CP-D facies are characterized by fine lamination, disruption by polygonal mudcracks and pedogenic processes. This suggests that the carbonate-rich pools were probably sitting in a dry sheet-washed mudflat in the sense of Hardie et al. (1978) dominated by sheetflood processes. Similar

Fig. 4. Photographs of the Cerro Puntudo Formation oncolitic limestones (Lo facies), Cuyana Basin, NW Argentina. A) Field photograph of a thick oncolitic limestone with inversely graded oncolites. Black arrows point to thin mud levels interbedded with the limestone. Stratigraphic position of photographed level is 24.5 m (See Fig 2). B) Polished slab of the oncolitic limestone. C) Thin section photograph of the filamentous algae remains distributed as tangled masses. D) Thin section photograph of the filaments radially disposed in the cortex of an oncolite. Thin sections C and D belong to a stratigraphic level located between 19 and 21 m (Fig. 2). E) Thin section photograph of a gyrogonite associated to articulated thalli. The white arrows point to the thalli nodes. Thin section is from the 22 m level in the stratigraphic section. F) Thin section photograph of the longitudinal section of a gyrogonite where external wall cells can be observed. G) Thin section photograph of the tangential section of a recrystallized gyrogonite. The white arrow points to the apical neck with slightly vertically bent projections. Thin sections F and G belong to a particular oncolitic limestone level located at 24.5 m in the stratigraphic section (Fig. 2). H) Thin section photograph of articulated ostracode valves in the micritic matrix.


A
100 µm
B
50 µm
C
50 µm
D
200 µm
E
100 µm
F
50 µm
G
100 µm
H
S
C
100 µm

carbonate ponds from floodplains with sheetfloods in alluvial systems have been described by Gierlowski-Kordesch et al. (1991) and Sanz et al. (1995).

Tectonic setting of the basin as well as the drainage catchment area is crucial to understand hydrology patterns in a continental basin, including carbonate provenance (Gierlowski-Kordesch, 1998; Gierlowski-Kordesch et al., 2008; Pla-Pueyo et al., 2009). In this particular case, the calcium-rich input is sourced from Paleozoic limestone bedrock (Fig. 1) (Cardó and Díaz, 1999). These rocks could contribute significant amounts of calcium through either surface or groundwater input. Ca-rich catchment areas have been well documented as the source for carbonate lacustrine deposits (Gierlowski-Kordesch, 1998; Arenas et al., 2007; Jiang et al., 2007; Gierlowski-Kordesch, 2010). With respect to groundwater input, this is favored by tectonic faults and fracture zones (Gierlowski-Kordesch, 1998), where it can surge as springs (De Wet and Hubert, 1989; Casanova, 1994; Renaut and Tiercelin, 1994) along lake margins, at the fringes of alluvial fans (Nickel, 1985; Talbot, 1994), or at seeps directly into lakes (Liutkus et al., 2010). Unfortunately, as has been highlighted by Renaut and Tiercelin (1994), such hydrologic features rarely get preserved in the geologic record and are easily underestimated.

Oncolite facies (**Lo**) have been interpreted in previous reports as the infilling of channels in fluvio-lacustrine sequences (Alonso-Zarza et al., 1992; Vázquez-Urbez et al., 2002; Arenas et al., 2007). Also similar facies containing abundant and large phytoclasts with micrite coatings have been interpreted as the result of precipitation in carbonate fluvio-lacustrine and palustrine settings (Gierlowski-Kordesch et al., 1991; Alonso-Zarza et al., 1992; Vázquez-Urbez et al., 2002; Arenas et al., 2007; Alonso-Zarza and Wright, 2010; Arenas-Abad et al., 2010). However, in this case, sedimentary and paleobiologic evidence suggests preservation of the oncolites in the ponded settings which rules out a solely fluvial origin (Thrailkill, 1976; Risacher and Eugster, 1979). Risacher and Eugster (1979) actually corroborated pisolith formation and growth in stagnant and nearly stagnant spring-fed pools in Pastos Grandes, Bolivia. Similar charophyte dominant facies of a Cretaceous alluvial-lacustrine system have been interpreted by Gierlowski-Kordesch et al. (1991) as shallow lakes and ponds where carbonate precipitation was dominated by blue green algae with oncolites up to a decimeter in diameter. Moreover, recent spring-fed lakes containing stromatolites and oncoids, as well as *Chara* (charophyte algae) as aquatic associated vegetation, are observed in Cuatro Ciénagas, Coahuila, México (Winsborough, et al., 1994). Cuatro Ciénagas oncoids are mainly composed by filamentous algae like the oncolites described in this work and present a similar micro- and macrostructure of an alternating laminae pattern with filamentous algae radially disposed in the cortex. Also, a similar association of charophyte and epiphytic algae has been reported from the lacustrine paleoenvironment of the Lower Cretaceous of the Iberian Ranges in Spain. Charophyte thalli present epiphytic overgrowths that developed in stromatolite-like structures (Martín-Closas, 1999). It is probable that as they grew, thalli of the Cerro Puntudo charophytes were already covered by algae of epiphytic habit as well. This phenomenon has also been reported from observations in modern environments (Freytet and Verrecchia, 1998), and in this case is supported by the fact that vegetative structures are found articulated (Fig. 5C). Thalli, gyrogonites, and stems would have acted as a nucleus of precipitation favoring the colonization by microorganism and allowing the growth of small microbial mats. Subsequently, the encrusted charophytes were probably affected by moderate currents and minor energy that helped develop the oncolite cortex.

Paleobiologic evidence suggests that this facies was deposited subaqueously at the margins of a pond sourced by a spring or in a very shallow lacustrine setting. The oncolitic limestone facies (**Lo**) preserves an assemblage of charophytes (gyrogonites) and epiphytic microorganisms (microbial filaments) along with benthic fauna (sponges and ostracodes), narrowing the depositional interpretation as a ponded water paleoenvironment perhaps sourced by a spring or seep.

All the previous records of Triassic Charophyta correspond to Laurasia in the northern hemisphere (Martín-Closas et al., 2009). There are numerous reports from Europe, including Sweden (Horn af Ratzien, 1954), Germany (Breuer, 1988), Poland (Zatón et al., 2005), Slovenia (Martín-Closas et al., 2009), and a few from the USA (Peck and Eyer, 1963; Kietzke, 1989). Also there are abundant records from China (Wang and Huang, 1978; Huang, 1983). All of them are in a paleolatitudinal setting of approximately 50°N (Kutzbach and Gallimore, 1989; Parrish, 1993; Scotese et al., 1999; Sellwood and Valdes, 2006). This finding is approximately 45°S in Gondwana (Fig. 6), indicating that the taxon was equally distributed to the north and south. This is in agreement with the nearly symmetric disposition of Pangaea around the paleoequator during the Triassic (Parrish, 1993). In the southernmost point of the southern hemisphere (Patagonia), during the Triassic, a typical warm-temperate climate (dry summers–wet winters) is recognized by the reconstruction of phytogeographic provinces (Scotese et al., 1999; Quattrocchio et al., 2011). This record allows the expansion of the paleolatitudinal range of Charophyta towards the south and is indicative of a symmetric, paleogeographic distribution pattern around the equator.

The probable evolutionary stock for Triassic charophytes in Gondwana is closely associated to the Permian record from the Paraná Basin, Brazil. The taxonomic affinity of these Permian charophytes is the Porocharaceae family (Faria and Ricardi-Branco, 2009). This fact suggests a possible connection with the subsequent Triassic Porocharaceans described here. Despite this possible paleobiologic affinity, the paleogeographic and tectonic implications should be considered. The Brazilian Paraná Basin has been thought as disconnected in some degree from the Chaco–Paraná Argentinean Basin by the existence of the Asunción Arch (its south extension is still uncertain). Also the E basins of Argentina were disconnected from the basins located at the W active margin of Gondwana by an upland area (Limarino and Spalletti, 2006). Therefore, the possible dispersive pathways were restricted for the group. However, the comparison with the previous findings confirms the proposition of a poor record of the group during the Permian and the unique Porocharacean incursion into the Mesozoic (Martín-Closas, 2003).

6. Conclusions

The oncolitic limestone facies of the Cerro Puntudo Formation of the Cuyana Basin of northwest Argentina is interpreted as being deposited in a carbonate-rich pond environment. Ponds most likely developed in a low subsidence rate area of the rift, perhaps associated with springs, as part of a complex system of alluvial fan and carbonate fluvio-lacustrine environments in a rift setting. Calcium carbonate-rich water and the presence of microorganisms triggered the precipitation of micritic coatings and calcite around charophytes and stems forming the calcified microbial mats. Oncolite formation involved the growth of microbial mats above charophyte thalli. The precipitation of calcite and micrite was triggered by microbial activity and calcium

Fig. 5. Scanning electron microscope (SEM) photos of the Charophytes in the oncolitic limestones (**Lo**) of the Cerro Puntudo Formation of NW Argentina. A) Lateral view of a complete gyrogonite. The white arrow points to the neck-like apex. SE (secondary electron image). B) Detailed lateral view of the apex of the gyrogonite in A. The black arrow points to a probable pore in the apex. SE. C) Detailed view of the base of the gyrogonite in A. SE. D) Lateral view of a subprolate gyrogonite. SE. E) Lateral view of a fragment of a gyrogonite. The black arrow points to an apical pore. SE. F) Apical view of a fragment of a gyrogonite where a round pore can be seen (black arrow). SE. G) Apical view of a gyrogonite where a probably small pore is seen (black arrow). BSE (back scattered electron image). H) Transversal section of a gyrogonite. Differences in chemical composition – major inner calcite (c) and outer silica (s) components (rim like) – have been determined by energy-dispersive X-ray spectrometry (EDS); and are reflected in the different gray levels of the BSE image (Benavente et al., *personal communication*).

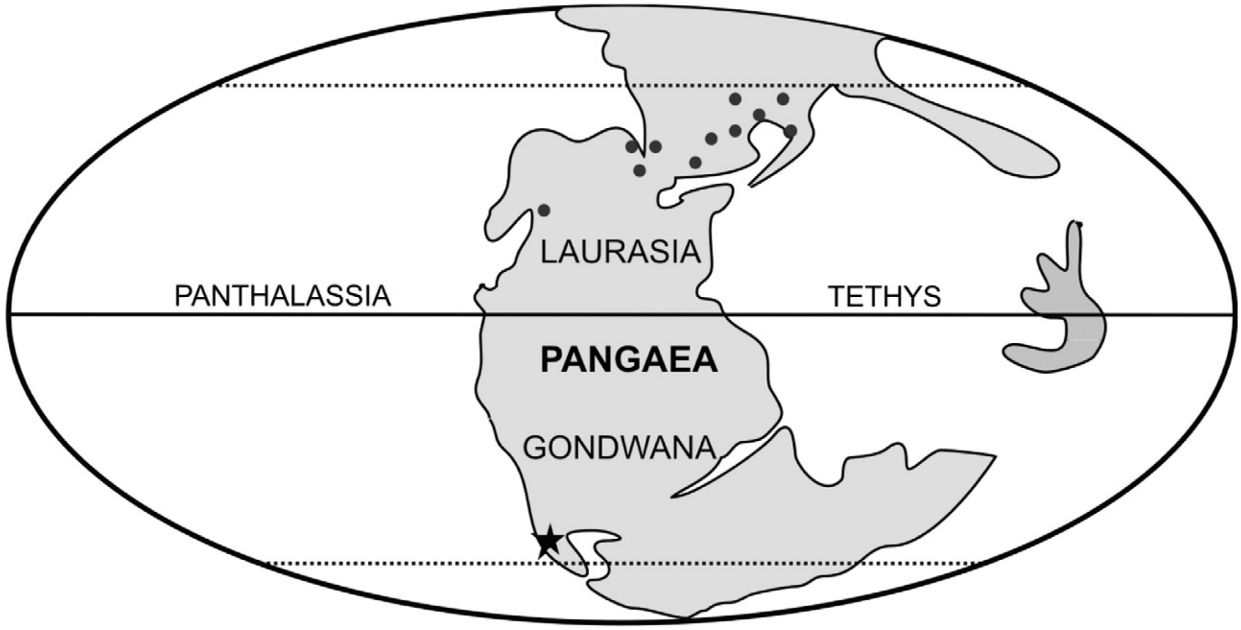


Fig. 6. Triassic paleogeographic map displaying Charophyta distribution in Pangaea. Small black dots are the main localities where the taxon has been found in Laurasia. Black star represents the new charophyte finding in Gondwana.

carbonate availability in the water. The existence of moderate energy currents and agitation may have promoted fragmentation of the material and the generation of abundant phytoclasts. Further research is needed to confirm carbonate provenance, and possible spring origin.

Charophytes found associated with the Cerro Puntudo paleolake constitute one of the scarce reports of the taxon for the Triassic, unique for the southern hemisphere. The paleolatitudinal location of this finding widens taxon distribution southwards into Gondwana, allowing the expansion of the paleobiogeographic distribution of the taxon up to 45°S. This paleolatitudinal range is similar to the one in the northern hemisphere.

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