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Salviniales from the Late Cretaceous of the Golfo San Jorge Basin

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ABSTRACT

The freshwater ferns (Salviniales) are well represented in the Maastrichtian deposits of Cerro de los Fragmentos in the headwaters of the Río Chico, Golfo San Jorge Basin. The fossil material of Salviniaceae includes complete megaspore apparatuses with attached microspore massulae and dispersed megaspores, float systems and microspore massulae of *Azolla*. The new species *Azolla colhuehuapensis* displays distinctive morphological characters including relative small megaspore apparatuses with easily detached floats and usually attached eglochidiate massulae. The Marsileaceae are represented by the megaspore *Molaspora lobata*, microspores of *Crybelosporites* and vegetative remains of *Marsileaceaephyllum* sp. The assemblage also includes zygospores of the green filamentous algae Zygnemataceae, spores of Marchantiophyta and Monilophyta (Schizaeales), megaspores of Isoetalean affinity and Palm-type angiosperm pollen grains. All these organic microfossils and the associated palynomorphs indicate the presence of a freshwater environment where abundant water ferns were developing and reproducing.

1. Introduction

The water ferns are a monophyletic group within the Order Salviniales Britton (Smith et al., 2006) and include the extant families Salviniaceae Martinov and Marsileaceae Mirbel (Smith et al., 2006; Christenhusz et al., 2011). They represent an important step in the evolution of modern heterospory, including for the first time since the origin of this reproductive strategy in the Palaeozoic, a single megaspore per megasporangium (a seed-like structure) (Nagalingum et al., 2006). They also present the most complex reproductive structures of the heterosporous plants, represented by the megaspores of the Salviniaceae (Hall, 1974; Batten and Collinson, 2001). They evolved in the Late Jurassic and diversified in the Late Cretaceous, with an excellent fossil record consisting of megaspores, microspores and vegetative remains (Lupia et al., 2000; Yamada and Kato, 2002; Martín-Closas, 2003; Vajda and McLoughlin, 2005; Nagalingum et al., 2006; Batten et al., 2011; Collinson et al., 2013). The water ferns are significant palaeoenvironmental indicators of fresh open-waters (photic zone) or wetlands (Collinson et al., 2013), with the extant Salviniaceae (*Azolla* and *Salvinia*) representing floating plants while the extant Marsileaceae (*Marsilea*, *Pilularia* and *Regnellidium*) include rhizomatous, semi-aquatic plants (Tryon and Tryon, 1982).

Salviniaceae from the Upper Cretaceous Patagonian deposits of Argentina include megaspore apparatuses and massulae of *Paleoazolla patagonica* Archangelsky et al., 1999 from the La Colonia Formation (Archangelsky et al., 1999; Cúneo et al., 2013, 2014) and dispersed massulae of *Azolla*, the latter including *A. cretacea* Stanley, 1965, *A.* (Rhizosperma) sp., *Azollopsis polyancyra* (Stough) Sweet and Hills, 1974, *A. circinata* Oltz and Hall, in Hall (1968) and *A.* spp. reported from the Loncoche, Allen and Paso del Sapo formations in Mendoza, Neuquén and Chubut provinces (Papú, 1988, 2002; Vallati, 2010; Puebla et al., 2014). Massulae of *Azollopsis polyancyra* have been also reported from the Upper Cretaceous deposits of the Austral Basin (Stough, 1968; Marenssi et al., 2004). The Marsileaceae megaspore *Molaspora lobata* (Dijkstra) Hall, in Hall and Peake (1968) and microspores of *Crybelosporites* have been reported from the La Colonia Formation (Cúneo et al., 2013; Cúneo et al., 2014; Hermsen et al., 2014).

The Upper Cretaceous megafossil record of Marsileaceae in Argentina includes leaves, leaflets, rhizomes and associated sporocarps from the La Colonia Formation of the Chubut province (Cúneo et al., 2013; Cúneo et al., 2014; Hermsen et al., 2014) and leaflets, rhizomes, roots, and a sporocarp-like structure from the Loncoche Formation of the Mendoza Province (Puebla et al., 2014).

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Salvinialean fossil remains consisting of massulae with septate glochidia, a single megaspore apparatus of *Azolla* and microspores of *Gabonisporis vigourouxii* Boltenhagen, 1967 have been reported from the uppermost part of the Lago Colhué Huapi Formation from a section outcropping at the headwaters of the Río Chico (Vallati et al., 2016). This palynoflora, included significant biostratigraphic markers of the upper Maastrichtian such as *Quadraplanus brossus* Stover and Partridge, 1973 and *Tubulifloridites lilliei* (Couper) Farabee and Canright, 1986.

In the present paper, we report additional aquatic plant material of the Salviniales from a nearby section at the headwaters of the Río Chico. The fossils include megaspore apparatuses, dispersed megaspores and massulae of the Salviniaceae as well as megaspores, microspores and vegetative remains of the Marsileaceae.

2. Geological setting

The Lago Colhué Huapi Formation was defined by Casal et al. (2015) for the lithostratigraphic interval in the uppermost part of the Chubut Group (Lesta and Ferello, 1972), which represents the main sedimentary filling in the Golfo San Jorge Basin (Fig. 1A–B). This unit overlies the Bajo Barreal Formation and underlies the Laguna Palacios Formation or the Salamanca Formation, according to its geographic position in the basin. The Lago Colhué Huapi Formation shows gradational top and basal contacts and occasionally an erosion surface (local unconformity) separates this unit from the Salamanca Formation (Casal et al., 2015; Vallati et al., 2016). In addition, at the studied locality (Fig. 1C), a laterally discontinuous basalt flow with a radiometric age of 67.31 ± 0.55 Ma (La Angostura Basalt) lies on top of the Lago Colhué Huapi Formation (Clyde et al., 2014).

The Cretaceous clastic and volcanoclastic deposits of the Chubut Group were interpreted as fluvio-lacustrine and fluvial systems. At its type locality, the Lago Colhué Huapi Formation, represents fluvial conditions of deposition with high-sinuosity channel systems and wide well-drained floodplains (Allard and Casal, 2013; Casal et al., 2015). This unit includes remains of titanosaurids, hadrosaurids and rare theropods (Casal et al., 2016), as well as plant remains (palynoflora, mesofossils and leaves) at the uppermost beds (Vallati et al., 2016; this paper).

The studied section, informally named Cerro de los Fragmentos, is a reduced outcrop (15 m thick), with an upward decreasing grain-size trend. It mainly includes medium to fine-grained sandstones that are interbedded with the reddish mudstones that characterize the Lago Colhué Huapi Formation (Fig. 2A–D). The high-sinuosity channel deposits recognized at Cerro de los Fragmentos are laterally related to proximal floodplain facies. The latter are represented by sandy to sandy-mud bodies of tabular geometry (sheet-like deposits) or flat-convex geometry (lobular deposits), as well as thin lentiform beds related to fluvial overflow. Furthermore, the red mudstones represent the deposits of distal floodplains, with the occasional presence of lagoon bodies (Casal et al., 2015).

This studied locality includes two fertile levels in the upper part of the Lago Colhué Huapi Formation. The lower layer (CF1 in Fig. 2A, D) contains the megaspores and the palynoflora presented herein. It is formed by grey fine to very fine-grained sandstones and limolites, up to 1 m thick, and with a lateral extension of tens of metres. This lithofacies is interpreted as a sheet-like non-channelized deposit. The upper layer containing the megafossil remains here reported, with the leaves of *Marsileaceaephyllum* (CF2 in Fig. 2A, C), is less than 10 cm thick, and overlies an erosion surface. The yellowish medium-grained sandstones, which are badly sorted, include plant remains with a disordered arrangement. This upper layer is a sheet-like deposit interpreted herein as the result of a high-density flow.

3. Materials and methods

3.1. Sample processing and study

The megaspores, palynomorphs and plant remains of the Salviniales were obtained from the beds CF1 and CF2 at Cerro de los Fragmentos in the headwaters of the Río Chico (Fig. 2A–D).

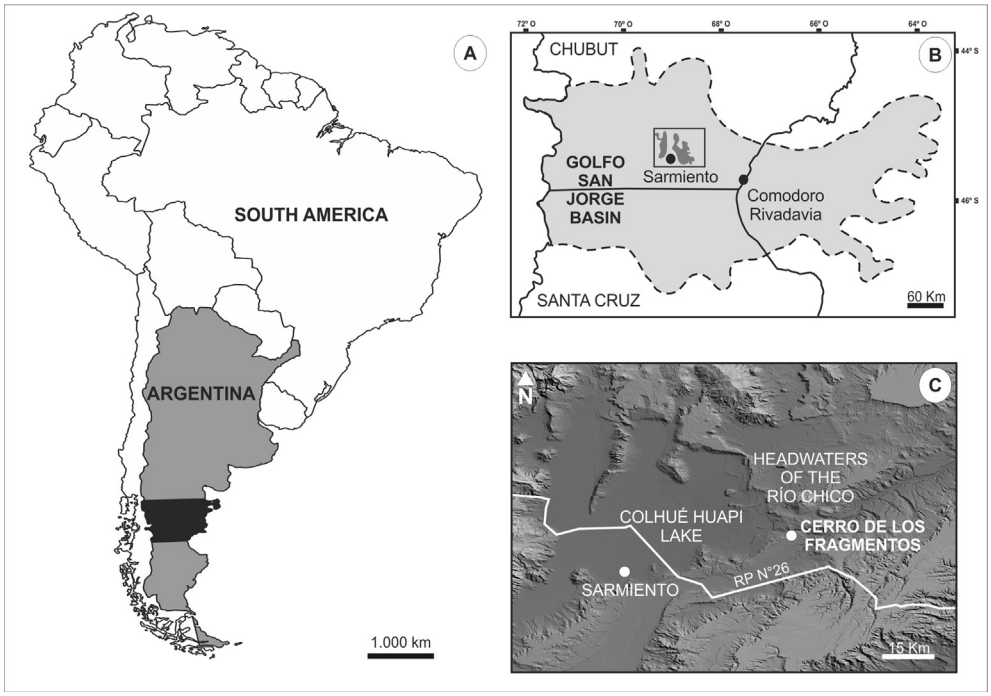

Fig. 1. Location map showing the studied locality Cerro de los Fragmentos in the headwaters of the Río Chico, Golfo San Jorge Basin.