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Insight into cretaceous floras: a synthesis from plant microfossils of the Chubut Group in the Golfo San Jorge Basin

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ABSTRACT

This study provides a comprehensive review of the key advances in micropaleontological research of the Chubut Group in the Golfo San Jorge Basin during the twenty-first century, with a particular emphasis on the plant microfossil record of two critical stratigraphic units: the Pozo D-129 Formation and the Lago Colhué Huapi Formation. The Pozo D-129 Formation, which outcrops at the Sierra Silva anticline, contains gyrogonites and utricles belonging to the Characeae and Clavatoraceae families, as well as a palynoflora assemblage that includes primitive angiosperm pollen grains. The analyzed microfossil assemblages suggest a late early Aptian age for these deposits and provide valuable insights into the freshwater paleoenvironment, which developed under semiarid conditions. In contrast, the microfossil record from the upper levels of the Lago Colhué Huapi Formation, recovered from outcrops at the headwaters of the Río Chico, did not yield charophytes but revealed rich palynological assemblages, including several megaspores from the orders Salviniales, Isoetales, and Selaginellales, along with additional palaeobotanical remains such as charcoal. These findings significantly contribute to interpreting a late Maastrichtian age and facilitate the reconstruction of the vegetation that thrived in freshwater environments under warm and humid climatic conditions.

Keywords: Charophytes, Palynomorphs, Pozo D-129 Formation, Lago Colhué Huapi Formation, paleoecological reconstruction

INTRODUCTION

Micropaleontology is a fundamental tool in biostratigraphic studies and plays a critical role in the paleoenvironmental and paleoecological interpretation of fertile deposits. Since the late twentieth century, numerous contributions have addressed palynomorphs and charophytes from both subsurface and surface rocks of the Chubut Group in the Golfo San Jorge Basin (Fig. 1A and B). Among these, pioneering biostratigraphic analyses in various stratigraphic units stand out.

A key milestone was the biozonation proposed by Archangelsky et al. (1984), based on the distribution of palynomorph species in several wells across southern Argentina. This analysis revealed that at least part of the Pozo D-129 Formation belongs to the Aptian *Antulsporites*–*Clavatipollenites* Zone of the Austral Basin. Similarly, Hechem et al. (1987) assigned an Aptian age to the formation, relying on a charophyte assemblage identified in Sierra Silva anticline exposures. In adjacent levels of the same section, Vallati (1996) reported a Barremian?–Aptian palynological assemblage, featuring scarce primitive angiosperm pollen grains.

Further refining the chronology, Barreda et al. (2003) documented a Barremian palynoflora at the Pozo D-129 Formation type locality (D-129 well), characterized by dominant coniferous pollen grains and low spore diversity. Later, Pérez Loinaze et al. (2019) examined subsurface samples from the south flank of the basin, recovering a microflora indicative of the initial phase of angiosperm diversification in Argentinean basins, to which a Barremian–early Aptian age was assigned.

Notably, Van Nieuwenhuise and Ormiston (1989) analyzed subsurface samples from the Pozo D-129 Formation and other Early Cretaceous units of the Golfo San Jorge Basin, proposing a model of saline-alkaline lakes under semi-arid climatic conditions. This interpretation aligns with the dominance of *Classopollis* pollen grains across nearly all the analyzed fertile samples.

In addition, Archangelsky et al. (1994) reported a palynological assemblage from younger levels of the Chubut Group, corresponding to the lower Caleta Olivia Member of the Cañadón Seco Formation (equivalent to the Lower Member of the Bajo Barreal Formation). This microflora, containing eudicotyledonous angiosperms, was assigned to the late Albian–Cenomanian interval and suggested the existence of shallow, calm freshwater bodies under a humid, temperate to warm climate.

More recently, Pérez Loinaze et al. (2021) analyzed samples from the uppermost member of the same formation (La Frieda Oeste x-1 well), identifying a Turonian–Coniacian palynoflora. This assemblage, which included advanced triporate and syncolporate pollen grains, suggested temperate to warm and humid conditions.

The scarcity of micropaleontological research focusing on paleoecological and paleoclimatic interpretations of the Chubut Group has limited the understanding of depositional environments and ecological evolution during much of the Cretaceous in central Patagonia. This gap underscores the need for more comprehensive and updated analyses.

In recent decades, several studies have examined outcrops of two key formations within the group: the lacustrine Pozo D-129 Formation and the fluvial Lago Colhué Huapi Formation (Vallati, 2013; Vallati et al., 2016, 2017, 2020; De Sosa Tomas et al., 2023). These formations, respectively the basal and upper units of the Chubut Group (Fig. 1B), host a microfossil record predominantly composed of reproductive plant structures (charophytes, palynomorphs, megaspores) and charred plant fragments.

This contribution emphasizes the biostratigraphic and paleoecological significance of these plant-derived microfossils. The paleoenvironmental reconstructions of both formations, complemented by earlier findings from the Cañadón Seco Formation, provide hypothetical snapshots of plant communities and deepen our understanding of ecological dynamics in central Patagonia during the Cretaceous.

THE CHUBUT GROUP IN THE GOLFO SAN JORGE BASIN

The Chubut Group, predominantly exposed in the San Bernardo fold belt, hosts the principal source rocks and hydrocarbon reservoirs of the Golfo San Jorge Basin. This lithostratigraphic unit is distinguished by lacustrine and fluvio-lacustrine deposits, with variable volcanic ash contributions, developed during the Barremian–Maastrichtian chronostratigraphic interval. The group comprises, in chronological order, the Pozo D-129, Matasiete, Castillo, Bajo Barreal, Laguna Palacios, and Lago Colhué Huapi formations. The basal and upper units yielded the plant microfossils analyzed in this contribution.

The Pozo D-129 Formation, primarily represented in the subsurface, constitutes the main source rock of the Golfo San Jorge Basin. The fertile samples examined come from the upper part of the unit, which outcrops at the Cerro Chenques section, within the Sierra Silva anticline (Fig. 1C and D).

The basal levels studied at this site (45° 17' 38.33" S; 69° 1' 2.25" W), where charophytes were recovered (De Sosa Tomas et al., 2023), consist of bluish-green siltstones with a high tuffaceous content, interbedded with brown-colored oolitic grainstones. The lithological succession occasionally features abundant gypsum and iron oxide concentrations, likely of secondary origin.

Upsection, the formation displays an increasing abundance of sandy layers and intercalated siltstones containing a well-preserved palynoflora (Vallati, 2013). The stratigraphic sequence culminates with the conglomeratic channels of the Matasiete Formation.

The Lago Colhué Huapi Formation predominantly comprises fluvial epiclastic deposits assigned to the Coniacian–Maastrichtian interval. It overlies the Bajo Barreal Formation and is in turn overlain by the marine Danian Salamanca Formation or the tuffaceous deposits of the Laguna Palacios Formation (Fig. 1B).

The upper levels of the Lago Colhué Huapi Formation (Fig. 1E), exposed at the headwaters of the Río Chico (45° 37' 24.90" S; 68° 26' 10.45" W), host well-diversified microfossil assemblages recovered from various sections, including Cerro del Hadro, Cerro de los Fragmentos, and Corral de Piedra (Fig. 1C).

The deposits exhibit a characteristic alternation of red mudstones and yellowish sandstones. Additionally, dark laminated siltstones and marlstone beds, interbedded within the sequence, contain the palynomorphs and megaspores analyzed in this study.

Figure 1. A) Relative location of the Golfo San Jorge Basin. **B)** Stratigraphic framework of the basin (adapted from Paredes et al., 2016). **C)** Location map of the key localities containing the microfossils discussed in this synthesis (modified from Paredes et al., 2016). Keys: yellow star: Sierra Silva, pink star: Cerro del Hadro, green star: Corral de Piedra, blue star: Cerro de los Fragmentos. **D)** Panoramic view of the study area at Sierra Silva. **E)** Panoramic view of the study area at the headwaters of the Río Chico.

THE MICROFOSSIL RECORD OF LAND PLANTS

We present here an up-to-date summary of the microfossils recorded in outcrops of the Pozo D-129 (Fig. 2A–F) and Lago Colhué Huapi (Fig. 2G–P) formations of the Chubut Group. The following list (Table 1) includes charophyte species and palynomorph taxa, systematically organized according to their composition into calcareous and organic-walled microfossils. Additionally, megaspores and charcoalified plant fragments are classified as mesofossils. These plant fossils, ranging in size from a few millimeters to one centimeter, represent an intermediate category between microfossils and macrofossils and require microscopic examination for detailed analysis.

The known or inferred plant affinities of these microfossils serve as a valuable proxy for interpreting the paleoenvironmental and paleoclimatic conditions that prevailed during the deposition of these fertile sedimentary units. The biostratigraphic significance of the microfossil assemblages is discussed in detail in the Discussion section.

DISCUSSION

Biostratigraphy and Paleobiogeography

Taxonomic analyses of plant microfossils conducted in the Chubut Group over recent decades have significantly enhanced our understanding of the chronostratigraphy of the unit and the diversity and evolutionary patterns of Cretaceous plant communities. The studied assemblages contain key biostratigraphic markers, supporting the assignment of an early Aptian–Maastrichtian interval for the deposits exposed in central Patagonia.

The charophyte floras of the Pozo D-129 Formation include species with broad geographic distributions (Fig. 2A–D), such as *Clavator harrisii* and *Mesochara stipitata*. Their presence not only increases the biostratigraphic value of

Patagonian charophytes in non-marine basins but also suggests the existence of intermittent intercontinental connections, facilitating the exchange of plant taxa across regions.

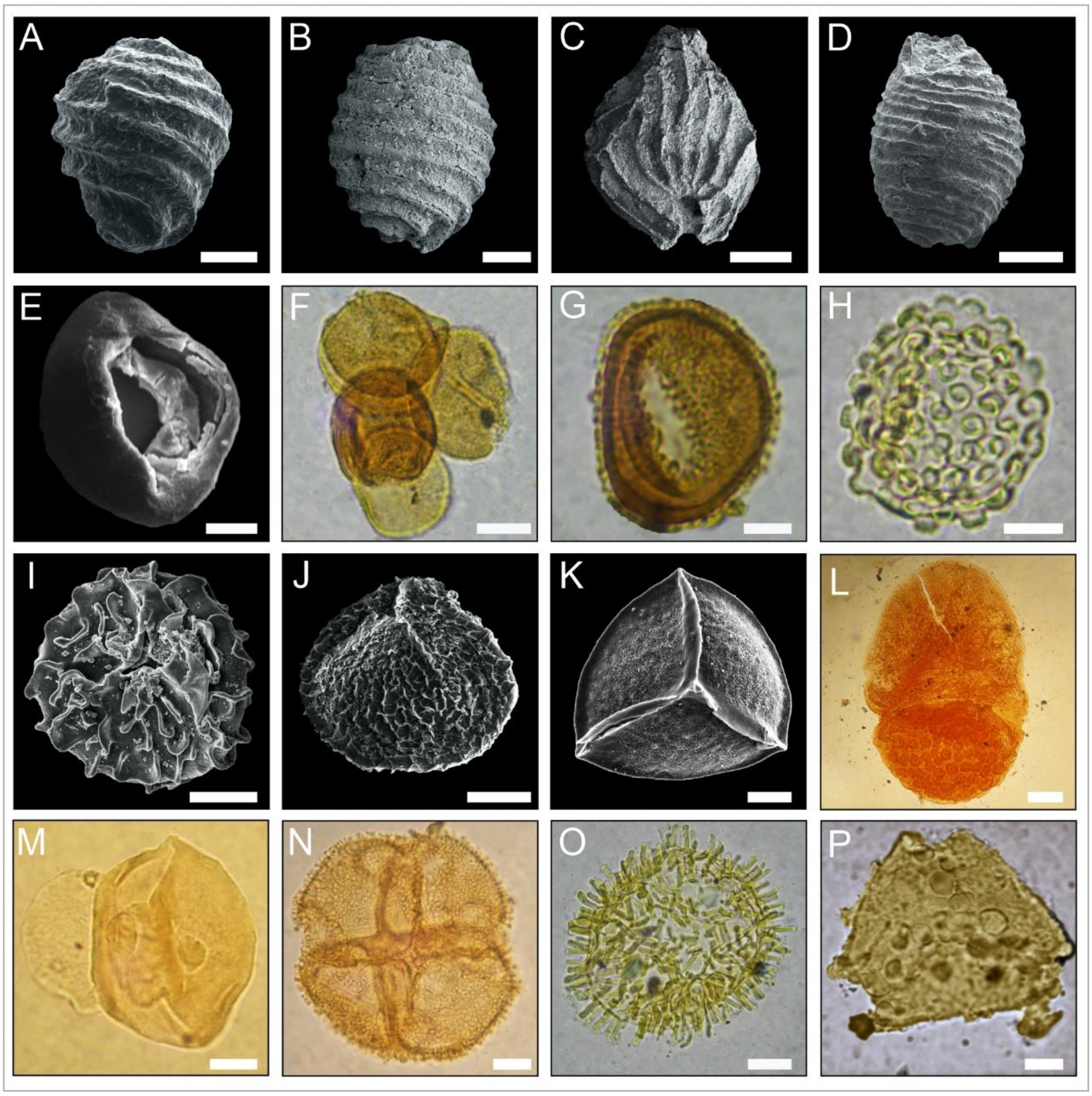

Figure 2. A–F. Selected microfossils from the Pozo D-129 Formation. **G–P.** Selected microfossils from the Lago Colhué Huapi Formation. **A.** *Mesochara stipitata*. **B.** *Lamprothamnium*? *barcinensis*. **C.** *Clavator harrisii* var. *harrisii*. **D.** *Clavator harrisii* var. *zavialensis*. **E.** *Cyclusphaera psilata.* **F.** *Tucanopollis crisopolensis* tetrad. **G.** *Clavatipollenites* sp. **H.** *Catinipollis geiseltalensis.* **I.** *Erlansonisporites* cf. *sparassis*. **J.** *Horstisporites*? sp. **K.** *Minerisporites* sp. **L.** *Azolla* sp.1. **M.** *Phyllocladidites mawsonii.* **N.** *Quadraplanus brossus.* **O.** *Spinizonocolpites riochiquensis*. **P.** *Beaupreaidites orbiculatus*. SEM micrographs (A–E, I–K), light microscope micrographs (F–H, L–P). Scale bars: A–B, K. 50 µm; C-D, I–K, L. 100 µm; F–H, M–P. 10 µm; L. 20 µm.

Pozo D-129 Formation at Sierra Silva Section

Calcareous microfossils	**Known or probable botanical affinity**
Clavator harrisii var. *harrisii*	Charophyta; Charales; Clavatoraceae
Clavator harrisii var. *zavialensis*	Charophyta; Charales; Clavatoraceae
Lamprothamnium? *barcinensis*	Charophyta; Charales; Characeae
Mesochara stipitata	Charophyta; Charales; Characeae
Organic-walled microfossils	
Aquatic palynomorphs	
Botryococcus sp.	Chlorophyta; Botryococcaceae
Ovoidites sp.	Streptophyta; Zygnematales; Zygnemataceae
Spores	
Antulsporites baculatus	Lycophyta; Sellaginellaceae
Biretisporites sp.1.	Monilophyta; Hymenophyllales; Hymenophyllaceae
Cicatricosisporites hughesii?	Monilophyta; Schizaeales; Schizaeceae
Cibotiumspora jurienensis	Monilophyta; Cyatheales
Densoisporites corrugatus	Lycophyta; Isoetales
Foraminisporis microgranulatus	Bryophyta; Nothothyladales; Notothyladaceae
Foraminisporis sp.	Bryophyta; Nothothyladales; Notothyladaceae
Gleicheniidites senonicus	Monilophyta; Gleicheniales; Gleicheniaceae
Interulobites intraverrucatus	Incertae sedis
Interulobites sp.	Incertae sedis
Laevigatosporites sp.	Monilophyta; Dipteridaceae?; Polypodiaceae?
Taurocusporites segmentatus	Bryophyta; Nothothyladales; Nothothyladaceae
Taurocusporites sp.	Bryophyta; Nothothyladales; Nothothyladaceae
Verrucosisporites sp.	Monilophyta; Filicopsida
“Gymnosperm” pollen grains	
Araucariacites australis	Spermatophyta; Coniferales; Araucariaceae
Balmeiopsis limbatus	Spermatophyta; Coniferales; Araucariaceae
Classopollis classoides	Spermatophyta; Coniferales; Cheirolepidiaceae
Classopollis simplex	Spermatophyta; Coniferales; Cheirolepidiaceae
Classopollis? sp.	Spermatophyta; Coniferales; Cheirolepidiaceae
Cyclusphaera annularis	Spermatophyta; Coniferales; Araucariaceae
Cyclusphaera crassa	Spermatophyta; Coniferales; Araucariaceae
Cyclusphaera psilata	Spermatophyta; Coniferales; Araucariaceae
Cyclusphaera radiata	Spermatophyta; Coniferales; Araucariaceae
Cycadopites nitidus	Spermatophyta; Cycadales
Podocarpidites cf. *futa*	Spermatophyta; Coniferales; Podocarpaceae
Angiosperm pollen grains	
Clavatipollenites hughesii	Antophyta; clado Chloranthaceae?
Retimonocolpites sp.	Antophyta; clado Chloranthaceae?; Monocots?
Retimonocolpites ? sp.	Antophyta; clado Chloranthaceae?; Monocots?
Stellatopollis sp.	Antophyta; incertae sedis
Tucanopollis crisopolensis	Antophyta; clado Chloranthaceae?-*Ceratophyllum*?

Lago Colhué Huapi Formation

Organic-walled microfossils	**Known or probable botanical affinity**
Aquatic palynomorphs	
Catinipollis geiseltalensis	Streptophyta; Zygnematales; Zygnemataceae
Ovoidites parvus	Streptophyta; Zygnematales; Zygnemataceae
Ovoidites spriggi	Streptophyta; Zygnematales; Zygnemataceae
Ovoidites sp.	Streptophyta; Zygnematales; Zygnemataceae
Schizosporis reticulatus	Streptophyta; Zygnematales; Zygnemataceae
Spores	
Ariadnaesporites micromedusus	Monilophyta; Salviniales; Salviniaceae
Azolla sp.2 (massula, Vallati et al., 2017)	Monilophyta; Salviniales; Salviniaceae
Azolla sp.3 (massula, Vallati et al., 2020)	Monilophyta; Salviniales; Salviniaceae
Baculatisporites comaumensis	Monilophyta; Osmundaceae?; Hymenophyllaceae?
Biretisporites sp.	Monilophyta; Hymenophyllales; Hymenophyllaceae
Camarozonosporites cf. *ohaiensis*	Lycophyta; Lycopsida
Ceratosporites equalis	Lycophyta; Selaginellales; Selaginellaceae
Cibotiidites tuberculiformis	Monilophyta; Filicopsida; Dicksoniaceae
Cibotiidites cf. *auriculatus*	Monilophyta; Filicopsida; Dicksoniaceae
Cibotiidites sp.	Monilophyta; Filicopsida; Dicksoniaceae
Cicatricosiporites sp	Monilophyta; Schizaeales; Schizaeceae
Cicatricosisporites sp. 1	Monilophyta; Schizaeales; Schizaeceae
Cicatricosisporites sp. 2	Monilophyta; Schizaeales; Schizaeceae
Concavisporites sp.	Monilophyta; Filicopsida
Crybelosporites sp.	Monilophyta; Salviniales; Marsileaceae
Cyathidites sp.	Monilophyta; Filicopsida
Gabonisporis vigourouxii	Monilophyta; Salviniales; Marsileaceae
Gleicheniidites senonicus	Monilophyta; Gleicheniales; Gleicheniaceae
Interulobites intraverrucatus	Incertae sedis
Retitriletes austroclavadites	Lycophyta; Lycopsida; Lycopodiaceae
Retitriletes sp.	Lycophyta; Lycopsida; Lycopodiaceae
Ruffordiaspora sp.	Monilophyta; Schizaeales; Schizaeceae
Zlivisporis reticulatus	Bryophyta; Marchantiales
“Gymnosperm” pollen grains	
Araucariacites australis	Spermatophyta; Coniferales; Araucariaceae
Classopolis classoides	Spermatophyta; Coniferales; Cheirolepidiaceae
Classopollis sp.	Spermatophyta; Coniferales; Cheirolepidiaceae
Cycadopites sp.	Spermatophyta; Cycadopsida
Dacrycarpites australiensis	Spermatophyta; Coniferales; Podocarpaceae
Dacrydiumites florinii	Spermatophyta; Coniferales; Podocarpaceae
Dilwynites granulatus	Spermatophyta; Coniferales; Araucariaceae
Gamerroites sp.	Spermatophyta; Coniferales; Podocarpaceae
Gnetaceaepollenites barghoornii	Spermatophyta; Gnetales
Inaperturopollenites sp.	Spermatophyta; Coniferales

Lago Colhué Huapi Formation

...continuation	
Microcachryiidites antarcticus	Spermatophyta; Coniferales; Podocarpaceae
Phyllocladidites mawsonii	Spermatophyta; Coniferales; Podocarpaceae
Phyllocladidites? sp.	Spermatophyta; Coniferales; Podocarpaceae
Podocarpidites ellipticus	Spermatophyta; Coniferales; Podocarpaceae
Podocarpidites cf. *elegans*	Spermatophyta; Coniferales; Podocarpaceae
Podocarpidites cf. *microreticuloidata*	Spermatophyta; Coniferales; Podocarpaceae
Podocarpidites cf. *parviauriculatus*	Spermatophyta; Coniferales; Podocarpaceae
Podocarpidites spp.	Spermatophyta; Coniferales; Podocarpaceae
Rugubivesiculites sp.	Spermatophyta; Coniferales
Trisaccites sp.	Spermatophyta; Coniferales; Podocarpaceae
Angiosperm pollen grains	
Arecipites sp.	Antophyta; Monocot; Arecaeae
Buttinia andreevi	Antophyta; Eudicot
Beaupreaidites cf. *elegansiformis*	Antophyta; Eudicot; Proteaceae (*Beauprea* -type)
Beaupreaidites orbiculatus	Antophyta; Eudicot; Proteaceae (*Beauprea* -type)
Ericipites scabratus	Antophyta; Eudicot; Ericaceae
Mauritiidites? sp.	Antophyta; Arecaceae; Calamoidea
Liliacidites cf. *kaitangataensis*	Antophyta; Monocot; Liliaceae
Liliacidites kaitangataensis	Antophyta; Monocot; Liliaceae
Liliacidites regularis	Antophyta; Monocot; Liliaceae
Liliacidites variegatus	Antophyta; Monocot; Liliaceae
Peninsulapollis gillii	Antophyta; Eudicot; Proteaceae (*Beauprea*-type)
Peninsulapollis truswelliae	Antophyta; Eudicot; Proteaceae
Proteacidites scaboratus	Antophyta; Eudicot; Proteaceae
Proteacidites cf. *scaboratus*	Antophyta; Eudicot; Proteaceae
Proxapertites sp.	Antophyta; Monocot; Araceae/Arecaceae
Quadraplanus brossus	Antophyta; Incertae sedis
Spinizonocolpites riochiquensis	Antophyta; Monocot; Arecaceae
Spinizonocolpites cf. *hialinus*	Antophyta; Monocot; Arecaceae
Tricolpites sp.	Antophyta; Eudicot
Tubulifloridites lilliei	Antophyta; Eudicot; Asteraceae
Mesofossils (Megaspores and Charcoalified remains)	
Azolla colhuehuapensis	Monilophyta; Salviniales; Salviniaceae
Azolla sp 1 (Vallati et al., 2017)	Monilophyta; Salviniales; Salviniaceae
Erlansonisporites cf. *sparassis*	Lycophyta, Selaginellales
Horstisporites cf. *harrisii*	Lycophyta, Selaginellales
Minerisporites spp.	Lycophyta, Isoetales
Molaspora lobata	Monilophyta; Salviniales; Marsileaceae
Charcoalified wood fragments	Spermatophyta; Coniferales
Charcoalified floral parts	Antophyta; Incertae sedis

Table 1. List of plant microfossil taxa identified in the Pozo D-129 Formation at Sierra Silva and the Lago Colhué Huapi Formation near the headwaters of the Río Chico. The table includes the known or probable botanical affinities of the dispersed spores and pollen grains (Vallati, 2013; Vallati et al., 2020; De Sosa Tomas et al., 2023, and references therein).

Of particular significance is the recognition of *Clavator harrisii* var. *zavialensis* (Fig. 2D), which first appeared in the Tethyan record during the late early Aptian (Pérez-Cano et al., 2023). Additionally, the discovery of the primitive angiosperm pollen species *Tucanopollis crisopolensis* (Fig. 2F), distributed in the Barremian–early Aptian of the paleoequatorial region (Doyle and Endress, 2018 and references therein), supports a late early Aptian age for the uppermost part of the Pozo D-129 Formation (Vallati, 2013; De Sosa Tomas et al., 2023).

The palynoflora also includes various species of the araucariacean genus *Cyclusphaera* (Table 1; Fig. 2E), a taxon with an almost exclusively Gondwanan distribution. Notably, *Cyclusphaera psilata* serves as a characteristic marker of a subprovince in the austral region (Volkheimer, 1980; Fig. 3A). The co-occurrence of *C. psilata* with paleoequatorial taxa, including *Tucanopollis crisopolensis* and *Stellatopollis*, suggests that the microfloras of Chubut province were part of a transitional paleofloristic region as early as the Aptian (Fig. 3A).

The palynoflora of the Lago Colhué Huapi Formation (Fig. 2G–P) further refines the chronostratigraphic framework, with the presence of *Quadraplanus brossus* (Fig. 2N), a Maastrichtian marker associated with the high-latitude *Nothofagidites*/*Proteacidites* Province. Additionally, *Tubulifloridites lilliei*, another austral end-Cretaceous key species, is present. This taxon is notable for its disappearance during the Cretaceous/Paleogene (K/Pg) extinction event.

The assemblage also contains characteristic Maastrichtian taxa of the paleotropical Palmae Province (Herngreen et al., 1996), such as *Buttinia andreevi* and *Gabonisporis vigorouxii* (Herngreen et al., 1996; Vajda and Bercovici, 2012), both of which also became extinct at the K/Pg boundary.

The combined palynological data not only supports a Maastrichtian age for the Lago Colhué Huapi Formation but also suggests the coexistence of mixed climatic conditions (Fig. 3B), reflecting transitional paleoenvironmental settings influenced by both austral and paleotropical floristic provinces.

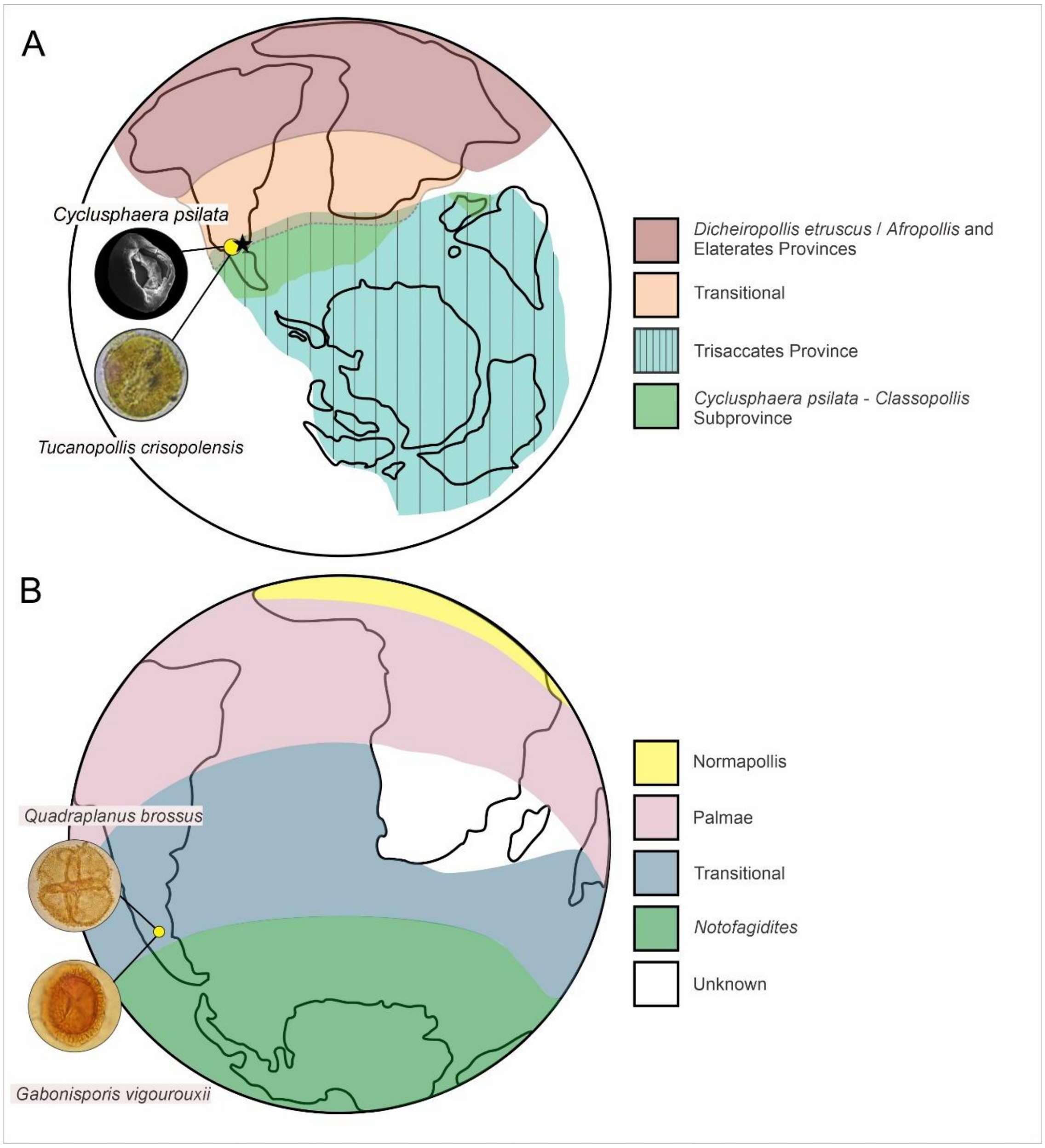

Figure 3. A. Early Cretaceous palynofloral provinces in the Southern Hemisphere. The relative position of the Pozo D-129 Formation outcrops at Sierra Silva is shown, with a yellow dot marking the presence of palynomorphs, and a black star indicating the occurrence of gyrogonites and utricles. The transitional palynofloral province has been extended southward to encompass this palynological assemblage (modified from Herngreen et al., 1996). **B.** Late Cretaceous palynofloral provinces in the Southern Hemisphere. The yellow dot marks the relative location of the fertile levels of the Lago Colhué Huapi Formation at the headwaters of the Río Chico (modified from Vajda and Bercovici, 2012).

Paleoecology and Paleoclimatology

Pozo D-129 Formation. The compositional differences observed in the two charophyte floras identified in the Pozo D-129 Formation at the Sierra Silva section are interpreted as reflecting distinct paleoenvironmental conditions (De Sosa Tomas et al., 2023). The lower assemblage represents temporary and unstable water bodies, which later evolved into more stable, permanent lacustrine environments, as evidenced by the upper assemblage.

The lower assemblage includes two characean taxa: *Mesochara stipitata* (Fig. 2A) and *Lamprothamnium*? *barcinensis* (Fig. 2B), both recorded for the first time in this basin, marking their southernmost distribution. *L.*? *barcinensis*, likely an endemic species, was initially described in the Early Cretaceous of the Cañadón Asfalto Basin (De Sosa Tomas et al., 2017).

Given that extant species of *Lamprothamnium* typically inhabit brackish, saline, and hypersaline environments (Soulié-Märsche, 2008), its presence in both assemblages of the Pozo D-129 Formation have notable paleoecological implications. Furthermore, the production of gyrogonites by *Lamprothamnium* under salinity levels of 20–40 g/l highlights its potential utility in paleosalinity reconstructions. The gyrogonites recovered from the lower levels are small in size and associated with freshwater ostracods and gastropods (De Sosa Tomas et al., 2023).

The poorly diversified assemblage, with diminutive fructifications, is interpreted as representing a littoral environment subject to seasonal water-level fluctuations. Supporting this interpretation, Carignano et al. (2017) linked the abundance of the opportunistic ostracod species *Damonella ultima* —noted for its tolerance to abrupt seasonal changes— to stressful paleoenvironmental conditions at this site.

The upper assemblage, found near the oolitic bed, comprises clavatoracean utricles of *Clavator harrisii* (*C. harrisii* var. *harrisii* and *C. harrisii* var. *zavialensis*, Figs. 2C, D) alongside gyrogonites of *Lamprothamnium*? *barcinensis* and charophyte thalli (De Sosa Tomas et al., 2023). This assemblage suggests a lacustrine coastal environment with substantial clastic input, as corroborated by the increasing abundance of coarse-grained facies toward the top of the section. In this sense, Pérez-Cano et al. (2022) characterized *Clavator harrisii* as a species well-adapted to clastic-rich lacustrine settings.

The palynoflora of the Pozo D-129 Formation is predominantly terrestrial, although aquatic palynomorphs, including *Botryococcus* (colonial green algae) and *Ovoidites* (filamentous algae), were also recorded, suggesting proximity to a lacustrine coastal zone. In wet and shaded areas near these water bodies (Fig. 4), bryophytes, lycophytes, and ferns (Monilophyta) likely thrived, as indicated by various spore types (Table 1).

The palynological assemblage is dominated by coniferous pollen grains, with *Classopollis* representing nearly 70% of the microflora. The predominance of *Classopollis*, produced by the Cheirolepidiaceae—an extinct family of xerophytic plants—suggests that the region experienced warm, semiarid conditions during the Early Cretaceous.

The Araucariaceae family is also well-diversified in the assemblage (Table 1). Kershaw and Wagstaff (2001) highlighted the paleoecological significance of this family, suggesting that its post-Permian/Triassic diversification was linked to arid climatic conditions prevalent across Gondwana. Although araucariaceans were widespread during the Mesozoic, their decline in the Late Cretaceous coincided with the rapid diversification of angiosperms.

Among the angiosperm taxa identified are *Tucanopollis* (Fig. 2F) and *Clavatipollenites* (Fig. 2G), both potentially related to the Chloranthaceae family (Doyle and Endress, 2018; Table 1). *Retimonocolpites*, also identified in the assemblage, has been associated with both the Chloranthaceae and Monocots (Friis et al., 2010; Doyle and Endress, 2018).

The Chloranthaceae family played a significant role in the Early Cretaceous angiosperm radiation. In particular, *Tucanopollis*, the most abundant angiosperm pollen taxon, is thought to be related to both Chloranthaceae and the aquatic genus *Ceratophyllum* (Doyle and Endress, 2018; Table 1).

Notably, a Cretaceous fossil plant from France and the Bohemian Basin (*Pseudoasterophyllites*), associated with *Tucanopollis* pollen (Kvaček et al., 2012), exhibits halophytic characteristics. Should the presence of salt-tolerant plants ecologically similar to *Pseudoasterophyllites* be confirmed in the Early Cretaceous of central Patagonia, it would align with the hypothesis that the Pozo D-129 Formation was deposited in a saline-alkaline lake under semiarid conditions, as previously suggested by Van Nieuwenhuise and Ormiston (1989).

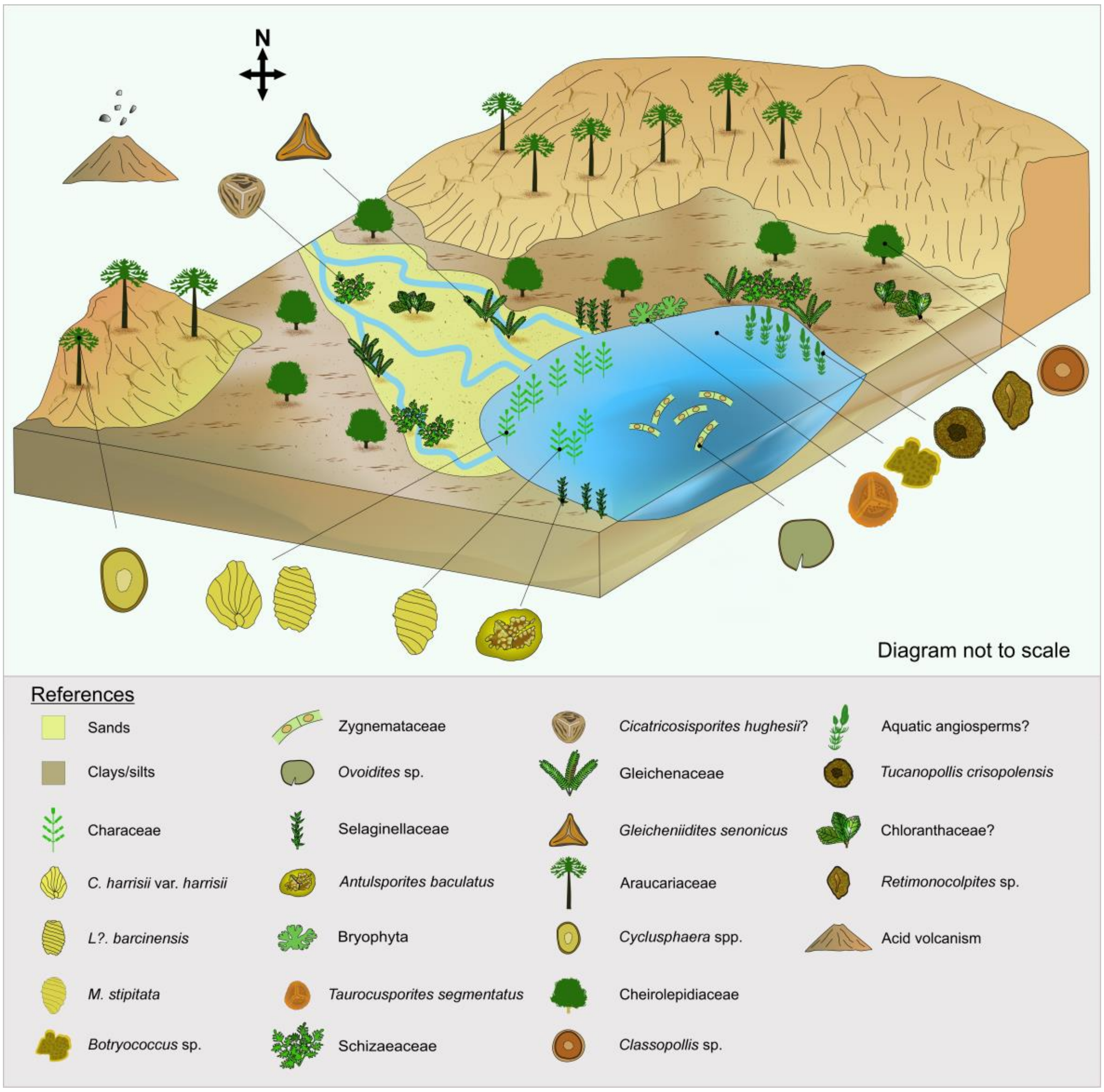

Figure 4. Paleoenvironmental reconstruction of the Pozo D-129 Formation at Sierra Silva, based on the analysis of charophytes and palynomorphs. The topographically elevated areas may correspond either to Paleozoic igneous-metamorphic basement rocks or to volcanic units of the Bahía Laura Volcanic Complex and its equivalents (Miller and Marino, 2019).

Lago Colhué Huapi Formation. The palynoflora, along with megaspores of aquatic ferns and lycophytes identified in the Lago Colhué Huapi Formation, provides essential insights into the paleoenvironmental and paleoclimatic conditions that shaped central Patagonia during a critical interval in Earth's history.

The abundant presence of megaspores and microspores from the Order Salviniales, particularly *Azolla* spp. (Fig. 2L), serves as a key indicator of freshwater environments, such as the photic zone of open waters and wetlands. The occurrence of filamentous green algae (Zygnemataceae), represented by the zygospore *Catinipollis geiseltalensis* (Fig. 2H), suggests shallow, calm, warm, and well-oxygenated waters. These algae's reproductive cycles are likely influenced by seasonal climatic fluctuations.

Bryophytes of the *Riccia*-type and lycophytes, represented by a diverse assemblage of microspores and megaspores (Fig. 2I–K), likely colonized riverbanks and lagoon margins under favorable environmental conditions. The vulnerability of extant lycophytes to environmental changes, due to their spore-based reproduction, slow growth, and limited competitive strategies, indicates that the depositional environment experienced minimal stress during sedimentation.

Notably, Gamerro (1977) related the isoetacean genus *Minerisporites* (Fig. 2K), well represented in the Lago Colhué Huapi Formation, to extant *Isoetes*. These plants exhibit adaptations to seasonally flooded habitats, including the burial of leafless stems during dry periods, further supporting a seasonally dynamic paleoenvironment.

The Proteaceae family, including taxa such as *Proteacidites*, *Peninsulapollis*, and *Beaupreaidites* (Fig. 2P), likely developed in humid environments near watercourses. Of particular interest is the presence of *Beauprea*-type pollen (Table 1), which holds paleoclimatic significance. The thermophilic genus *Beauprea* disappeared from South America as climatic conditions shifted toward cooler and drier environments (Lamont et al., 2024). Today, *Beauprea* is confined to the humid, warm climates of New Caledonia, suggesting similar conditions may have prevailed in Maastrichtian Patagonia.

The Podocarpaceae, well-represented in the palynological assemblage (Table 1) and by charred plant remains, likely thrived in elevated areas, possibly linked to early tectonic inversion stages in the basin (Navarrete et al., 2015; Allard et al., 2020). Additionally, the abundant pollen species *Phyllocladidites mawsonii* (Fig. 2M) is associated with *Lagarostrobus franklinii* (Huon pine), a rainforest tree native to southern and western Tasmania (Bowman et al., 2014), indicating temperate rainforest conditions.

In the swampy alluvial plains, angiosperms with liliaceous affinities (*Liliacidites* spp.) likely flourished. Palm trees (Arecaceae) —typical of tropical and subtropical regions— are represented by various taxa in the palynological record. Of particular significance is the angiosperm pollen genus *Spinizonocolpites* (Fig. 2O), related to the modern *Nypa*-palm, a tropical species adapted to mangrove biomes (Harley and Baker, 2001). This relationship implies the potential presence of coastal saline or brackish water environments during the Maastrichtian (Fig. 5), where palms with similar ecological requirements could have thrived.

The occurrence of charcoal unequivocally indicates natural surface paleofires, which were common during the Cretaceous, partly due to elevated atmospheric oxygen levels. The identification of *Beauprea*-like pollen (Table 1) in the Maastrichtian deposits is notable, given that *Beauprea* possesses fire-adaptive traits, including seed storage mechanisms that facilitate regeneration in fire-prone environments (Lamont and He, 2012).

Vegetal charcoal, primarily recovered from a calcareous bed within the Lago Colhué Huapi Formation, includes coniferous wood (Vallati et al., 2020) and angiosperm fragments, such as a dithecous anther with longitudinal dehiscence (Vallati et al., 2018).

Moreover, the discovery of calcified stromatolites in the upper levels of the unit provides insights into the photic zone of the associated water bodies. These stromatolites, likely constructed by cyanobacteria, indicate microbial activity in shallow aquatic environments (Casal et al., 2020).

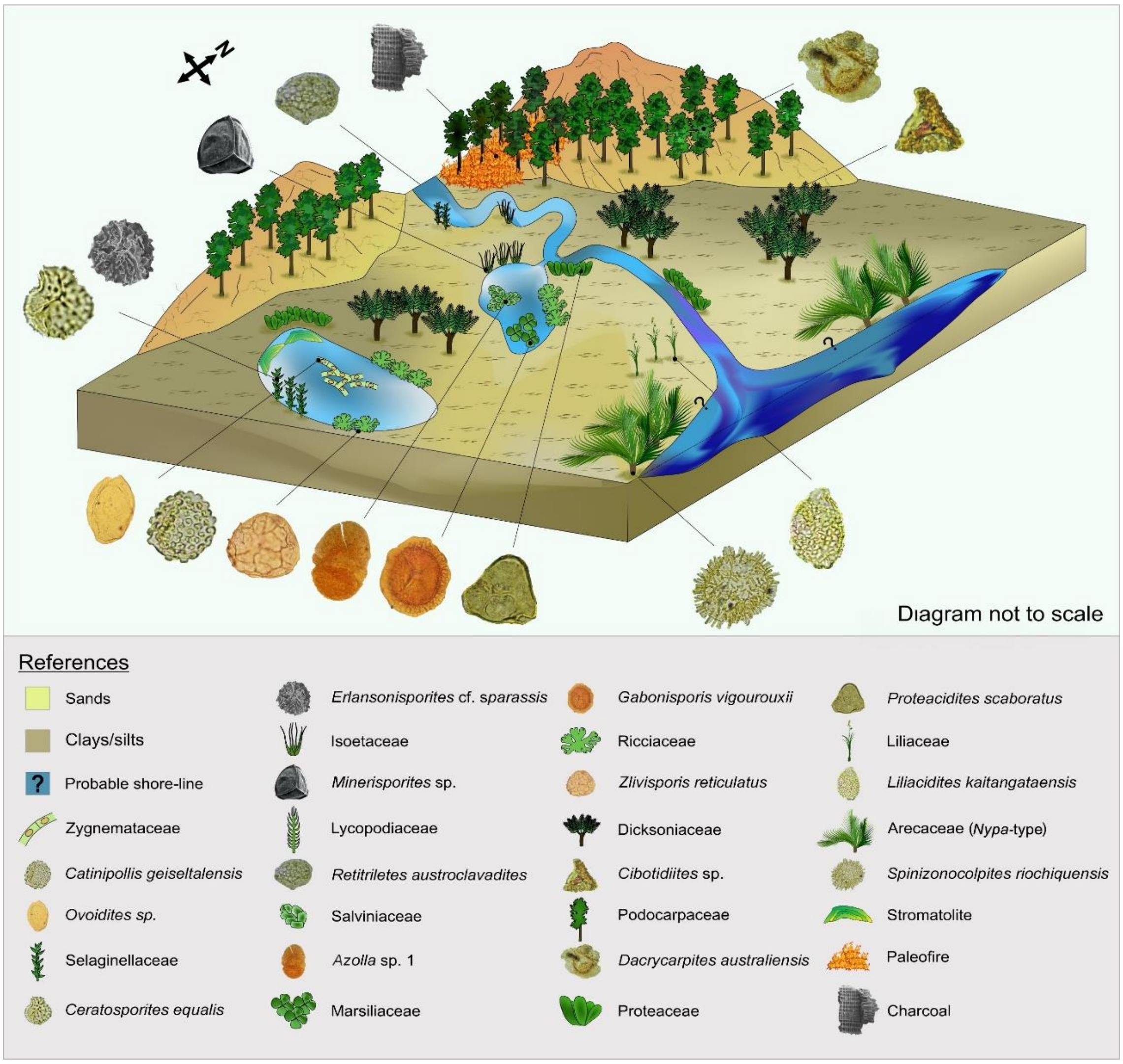

Figure 5. Paleoenvironmental reconstruction of the Lago Colhué Huapi Formation at the headwaters of the Río Chico, based on the analysis of palynomorphs and megaspores (modified from Vallati et al., 2020). The topographically elevated areas are likely associated with previously deposited rocks of the Chubut Group (Navarrete et al., 2015; Allard et al., 2020).

FINAL CONSIDERATIONS

The plant microfossils of the Chubut Group provide valuable evidence of the environmental and climatic transitions that occurred during the Cretaceous in central Patagonia.

During the early Aptian, a saline-alkaline lake developed under a warm, semiarid climate, characterized by seasonally fluctuating water levels. The littoral zone of this lake served as a habitat for salt-tolerant charophytes and probable halophytic angiosperms, which colonized the margins of the water body.

In contrast, wetter and milder climatic conditions prevailed during the late Albian–Coniacian interval, as reflected by microfloras representing a diverse assemblage of arboreal, subarboreal, and shrubby vegetation. These communities thrived in distal floodplain environments associated with water bodies.

By the end of the Cretaceous, a humid and warm climate, favored the development of a freshwater ecosystem, characterized by the proliferation of aquatic ferns and a rich surrounding vegetation. This scenario aligns with typical Maastrichtian assemblages documented across the Southern Hemisphere.

The observed paleoenvironmental transition likely reflects the influence of broader paleogeographic and climatic changes that shaped the evolution of regional vegetation and ecosystems in Patagonia during the Cretaceous.

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