

INSIGHT INTO CRETACEOUS FLORAS: A SYNTHESIS FROM PLANT MICROFOSSILS OF THE CHUBUT GROUP IN THE GOLFO SAN JORGE BASIN

Andrea De Sosa Tomas^{1*} , Patricia Vallati¹

¹ Laboratorio de Bioestratigrafía “Dr. Eduardo Musacchio”, Departamento de Geología, Universidad Nacional de la Patagonia San Juan Bosco, Ciudad, Universitaria Km. 4, Comodoro Rivadavia, Chubut, Argentina.

*Corresponding author: adesosatomas@gmail.com

ARTICLE INFO

Article history

Received October 17, 2024

Accepted March 3, 2025

Available online March 17, 2025

Handling (guest) Editor

José M. Paredes

Keywords

Charophytes

Palynomorphs

Pozo D-129 Formation

Lago Colhué Huapi Formation

Paleoecological reconstruction

ABSTRACT

This study provides a comprehensive review of 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 Salviniiales, 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.

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.

It is worth noting that 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 agrees 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 part 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 charcoalfied 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.

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. The species *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 *Quadruplanus 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 *Gabonispuris 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.

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

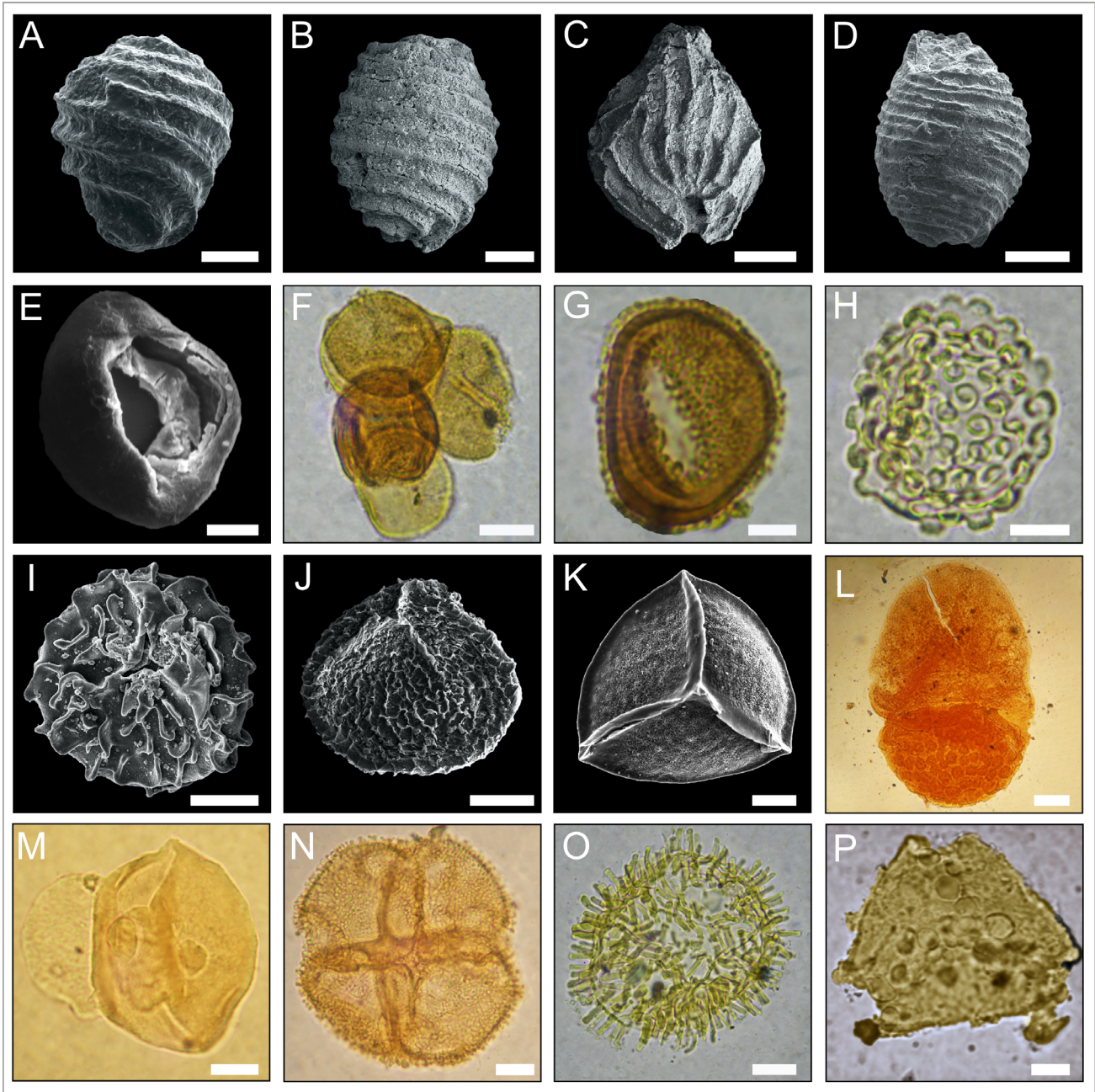


Figure 2. A–F) Selected microfossils from the Pozo D-129 Formation. G–L) Selected microfossils from the Lago Colhué Huapi Formation. A) *Mesochara stipitata*. B) *Lamprothamnium?* *barcinensis*. C) *Clavator harrisii* var. *harrisii*. D) *Clavator harrisii* var. *zavialensis*. E) *Cyclusphaera psilata*. 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) *Quadruplanus 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 .

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

Pozo D-129 Formation at Sierra Silva Section		Lago Colhué Huapi Formation		Lago Colhué Huapi Formation	
Calcareous microfossils	Known or probable botanical affinity	Organic-walled microfossils	Known or probable botanical affinity	...continuation	
<i>Clavator harrisi</i> var. <i>harrisi</i>	Charophyta; Charales; Clavatoraceae	Aquatic palynomorphs		<i>Microcaryonites antarcticus</i>	Spermatophyta; Coniferales; Podocarpaceae
<i>Clavator harrisi</i> var. <i>zavaiensis</i>	Charophyta; Charales; Clavatoraceae	<i>Catinipollis geiseliiensis</i>	Streptophyta; Zygnematales; Zygnemataceae	<i>Phyllocladites mawsonii</i>	Spermatophyta; Coniferales; Podocarpaceae
<i>Lamprothamnium? barcinensis</i>	Charophyta; Charales; Characeae	<i>Ovoidites parvus</i>	Streptophyta; Zygnematales; Zygnemataceae	<i>Phyllocladites? sp.</i>	Spermatophyta; Coniferales; Podocarpaceae
<i>Mesochora stipitata</i>	Charophyta; Charales; Characeae	<i>Ovoidites springi</i>	Streptophyta; Zygnematales; Zygnemataceae	<i>Podocarpidites ellipticus</i>	Spermatophyta; Coniferales; Podocarpaceae
Organic-walled microfossils		<i>Ovoidites sp.</i>	Streptophyta; Zygnematales; Zygnemataceae	<i>Podocarpidites cf. elegans</i>	Spermatophyta; Coniferales; Podocarpaceae
Aquatic palynomorphs		<i>Schizosporis reticulatus</i>	Streptophyta; Zygnematales; Zygnemataceae	<i>Podocarpidites cf. microreticuloidalis</i>	Spermatophyta; Coniferales; Podocarpaceae
<i>Botryococcus</i> sp.	Chlorophyta; Botryococcales	Spores		<i>Podocarpidites cf. parviauriculatus</i>	Spermatophyta; Coniferales; Podocarpaceae
<i>Ovoidites</i> sp.	Streptophyta; Zygnematales; Zygnemataceae	<i>Ariadnaesporites micromedusus</i>	Monilophyta; Salviniiales; Salviniaceae	<i>Podocarpidites</i> spp.	Spermatophyta; Coniferales; Podocarpaceae
Spores		<i>Azolla</i> sp. 2 (massuia, Vallati et al., 2017)	Monilophyta; Salviniiales; Salviniaceae	<i>Rugibrevicollites</i> sp.	Spermatophyta; Coniferales
<i>Antulisporites baculatus</i>	Lycophyta; Sellaginellaceae	<i>Azolla</i> sp. 3 (massuia, Vallati et al., 2020)	Monilophyta; Salviniiales; Salviniaceae	<i>Trisaccites</i> sp.	Spermatophyta; Coniferales; Podocarpaceae
<i>Biretisporites</i> sp. 1.	Monilophyta; Hymenophyllales; Hymenophyllaceae	<i>Baculatisporites conaumerensis</i>	Monilophyta; Osmundaceae?; Hymenophyllaceae?	Angiosperm pollen grains	
<i>Biretisporites hughesii?</i>	Monilophyta; Schizaeales; Schizaceae	<i>Biretisporites</i> sp.	Monilophyta; Hymenophyllales; Hymenophyllaceae	<i>Arecipites</i> sp.	Anthophyta; Monocot; Arecaeae
<i>Cibitolmspora jurenensis</i>	Monilophyta; Cyathales	<i>Camarozonosporites cf. ohatensis</i>	Lycophyta; Lycopodiaceae	<i>Butifina andreui</i>	Anthophyta; Eudicot
<i>Cicatricosporites corrugatus</i>	Lycophyta; Isoetales	<i>Ceratospores equalis</i>	Lycophyta; Selaginellales; Selaginellaceae	<i>Beaupreaidites cf. elegansiformis</i>	Anthophyta; Eudicot; Proteaceae (<i>Beauprea</i> -type)
<i>Densosporites microgranulatus</i>	Bryophyta; Notothyladales; Notothyladaceae	<i>Ciboidites tuberculiformis</i>	Monilophyta; Filicopsida; Dicksoniaceae	<i>Beaupreaidites orbiculatus</i>	Anthophyta; Eudicot; Proteaceae (<i>Beauprea</i> -type)
<i>Foraminisporis</i> sp.	Bryophyta; Notothyladales; Notothyladaceae	<i>Ciboidites cf. auriculatus</i>	Monilophyta; Filicopsida; Dicksoniaceae	<i>Ericipites scabratus</i>	Anthophyta; Eudicot; Ericaceae
<i>Gleicheniidites senonicus</i>	Monilophyta; Gleicheniales; Gleicheniaceae	<i>Ciboidites</i> sp.	Monilophyta; Filicopsida; Dicksoniaceae	<i>Mauritidites? sp.</i>	Anthophyta; Arecaeae; Calamoidae
<i>Intruilobites intraverrucatus</i>	Incertae sedis	<i>Cicatricosporites</i> sp.	Monilophyta; Schizaeales; Schizaceae	<i>Lilacitites cf. kaitangataensis</i>	Anthophyta; Monocot; Liliaceae
<i>Intruilobites</i> sp.	Incertae sedis	<i>Cicatricosporites</i> sp. 1	Monilophyta; Schizaeales; Schizaceae	<i>Lilacitites kaitangataensis</i>	Anthophyta; Monocot; Liliaceae
<i>Laevegatosporites</i> sp.	Monilophyta; Dipteridaceae?; Polypodiaceae?	<i>Cicatricosporites</i> sp. 2	Monilophyta; Schizaeales; Schizaceae	<i>Lilacitites regularis</i>	Anthophyta; Monocot; Liliaceae
<i>Tauroscusporites segmeritatus</i>	Bryophyta; Notothyladales; Notothyladaceae	<i>Concavisporites</i> sp.	Monilophyta; Filicopsida	<i>Lilacitites variegatus</i>	Anthophyta; Monocot; Liliaceae
<i>Tauroscusporites</i> sp.	Bryophyta; Notothyladales; Notothyladaceae	<i>Crybelosporites</i> sp.	Monilophyta; Salviniiales; Marsileaceae	<i>Perinisulapollis gillii</i>	Anthophyta; Eudicot; Proteaceae (<i>Beauprea</i> -type)
<i>Verrucosporites</i> sp.	Monilophyta; Filicopsida	<i>Cyathidites</i> sp.	Monilophyta; Filicopsida	<i>Perinisulapollis truswelliae</i>	Anthophyta; Eudicot; Proteaceae
"Gymnosperm" pollen grains		<i>Gabonsporites vigourouxii</i>	Monilophyta; Salviniiales; Marsileaceae	<i>Proteacidites scabratus</i>	Anthophyta; Eudicot; Proteaceae
<i>Araucariidites australis</i>	Spermatophyta; Coniferales; Araucariaceae	<i>Gleicheniidites senonicus</i>	Monilophyta; Gleicheniales; Gleicheniaceae	<i>Proteacidites cf. scabratus</i>	Anthophyta; Eudicot; Proteaceae
<i>Balmelopsis limbata</i>	Spermatophyta; Coniferales; Araucariaceae	<i>Intruilobites intraverrucatus</i>	Incertae sedis	<i>Proxaperites</i> sp.	Anthophyta; Monocot; Araceae/Araceae
<i>Classopollis classoides</i>	Spermatophyta; Coniferales; Cheirolepidiaceae	<i>Retriletes austroclavatus</i>	Lycophyta; Lycopodiaceae	<i>Quadraplanus brossus</i>	Anthophyta; Incertae sedis
<i>Classopollis simplex</i>	Spermatophyta; Coniferales; Cheirolepidiaceae	<i>Retriletes</i> sp.	Lycophyta; Lycopodiaceae	<i>Spinizonocolpites rochiquensis</i>	Anthophyta; Monocot; Araceae
<i>Classopollis? sp.</i>	Spermatophyta; Coniferales; Cheirolepidiaceae	<i>Ruffordiaspora</i> sp.	Monilophyta; Schizaeales; Schizaceae	<i>Spinizonocolpites cf. hialinus</i>	Anthophyta; Monocot; Araceae
<i>Cyclusphaera annularis</i>	Spermatophyta; Coniferales; Araucariaceae	<i>Zilvisporis reticulatus</i>	Bryophyta; Marchantiales	<i>Tricolpites</i> sp.	Anthophyta; Eudicot
<i>Cyclusphaera crassa</i>	Spermatophyta; Coniferales; Araucariaceae	"Gymnosperm" pollen grains		<i>Tubulifloridites lillei</i>	Anthophyta; Eudicot; Asteraceae
<i>Cyclusphaera psilata</i>	Spermatophyta; Coniferales; Araucariaceae	<i>Araucariidites australis</i>	Spermatophyta; Coniferales; Araucariaceae	Mesofossils (Megaspores and Charcoalified remains)	
<i>Cyclusphaera radiata</i>	Spermatophyta; Coniferales; Araucariaceae	<i>Classopollis classoides</i>	Spermatophyta; Coniferales; Cheirolepidiaceae	<i>Azolla colhuehuapiensis</i>	Monilophyta; Salviniiales; Salviniaceae
<i>Cycadoidites nitidus</i>	Spermatophyta; Cycadales	<i>Classopollis</i> sp.	Spermatophyta; Coniferales; Cheirolepidiaceae	<i>Azolla</i> sp. 1 (Vallati et al., 2017)	Monilophyta; Salviniiales; Salviniaceae
<i>Podocarpidites cf. titia</i>	Spermatophyta; Coniferales; Podocarpaceae	<i>Cycadoidites</i> sp.	Spermatophyta; Cycadopsida	<i>Erlansonisporites cf. sparassis</i>	Lycophyta; Selaginellales
Angiosperm pollen grains		<i>Dacrycarpites australis</i>	Spermatophyta; Coniferales; Podocarpaceae	<i>Horsatisporites cf. harrisi</i>	Lycophyta; Selaginellales
<i>Clavipollenites hughesii</i>	Anthophyta; clado Chloranthaceae?	<i>Dacrydulites florinii</i>	Spermatophyta; Coniferales; Podocarpaceae	<i>Minerisporites</i> spp.	Lycophyta; Isoetales
<i>Retimonocolpites</i> sp.	Anthophyta; clado Chloranthaceae?; Monocots?	<i>Dihytrites granulatus</i>	Spermatophyta; Coniferales; Araucariaceae	<i>Molasporea lobata</i>	Monilophyta; Salviniiales; Marsileaceae
<i>Retimonocolpites? sp.</i>	Anthophyta; clado Chloranthaceae?; Monocots?	<i>Gemerites</i> sp.	Spermatophyta; Coniferales; Podocarpaceae	Charcoalified wood fragments	Spermatophyta; Coniferales
<i>Stellatopollis</i> sp.	Anthophyta; Incertae sedis	<i>Gnetaceapollenites barghoornii</i>	Spermatophyta; Gnetales	Charcoalified floral parts	Anthophyta; Incertae sedis
<i>Tucanopollis crispolensis</i>	Anthophyta; clado Chloranthaceae?; Ceratophyllum?	<i>Inaperturopollenites</i> sp.	Spermatophyta; Coniferales		

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 Rio 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).

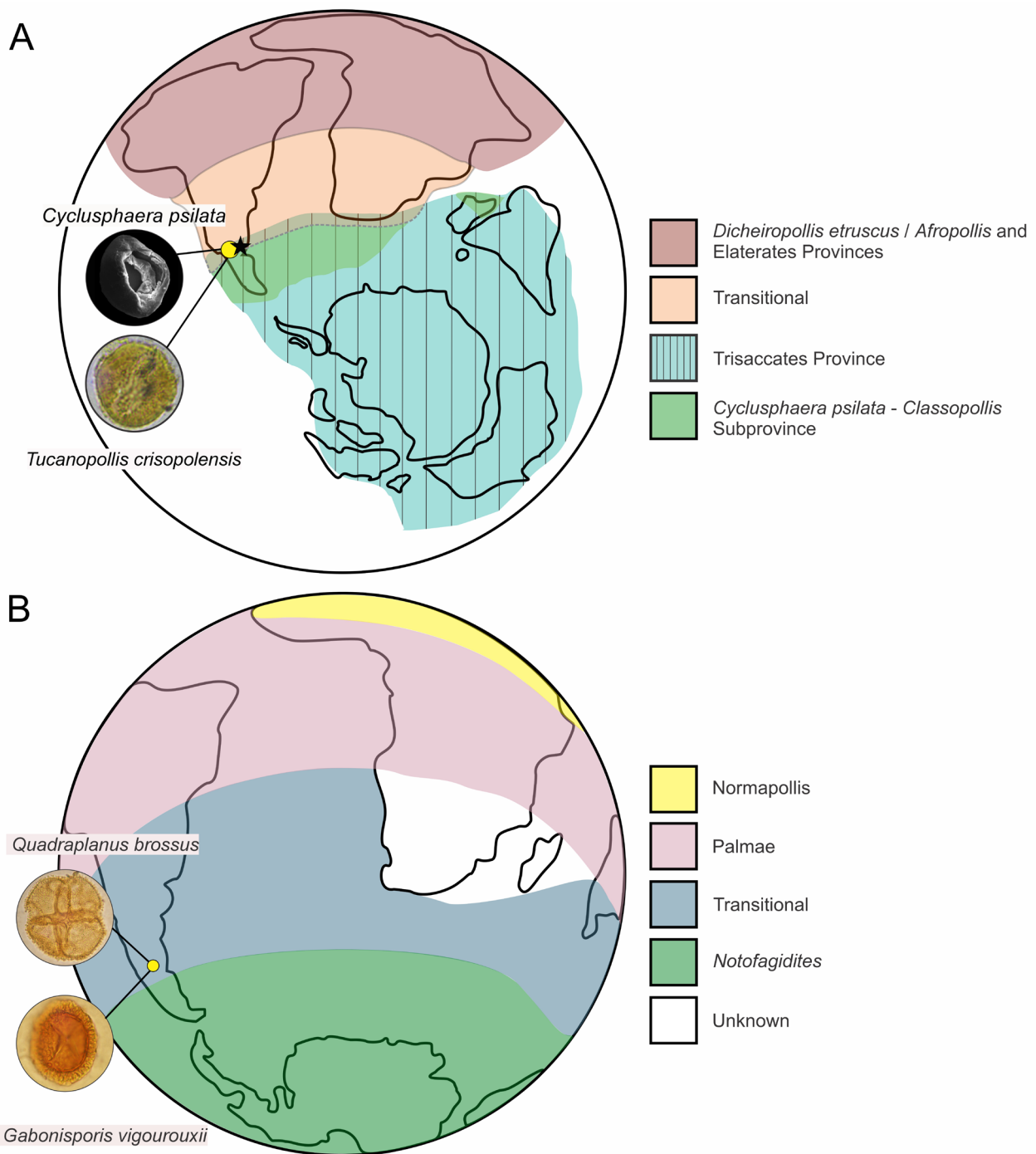


Figure 3. **A)** Early Cretaceous palynofloral provinces in the Southern Hemisphere. The relative position of the Pozo D-129 Formation outcrops at Sierra Silva is shown, with a yellow dot marking the presence of palynomorphs, and a black star indicating the occurrence of gyrogonites and utricles. The transitional palynofloral province has been extended southward to encompass this palynological assemblage (modified from Hengreen *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).

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 clavatorcean 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

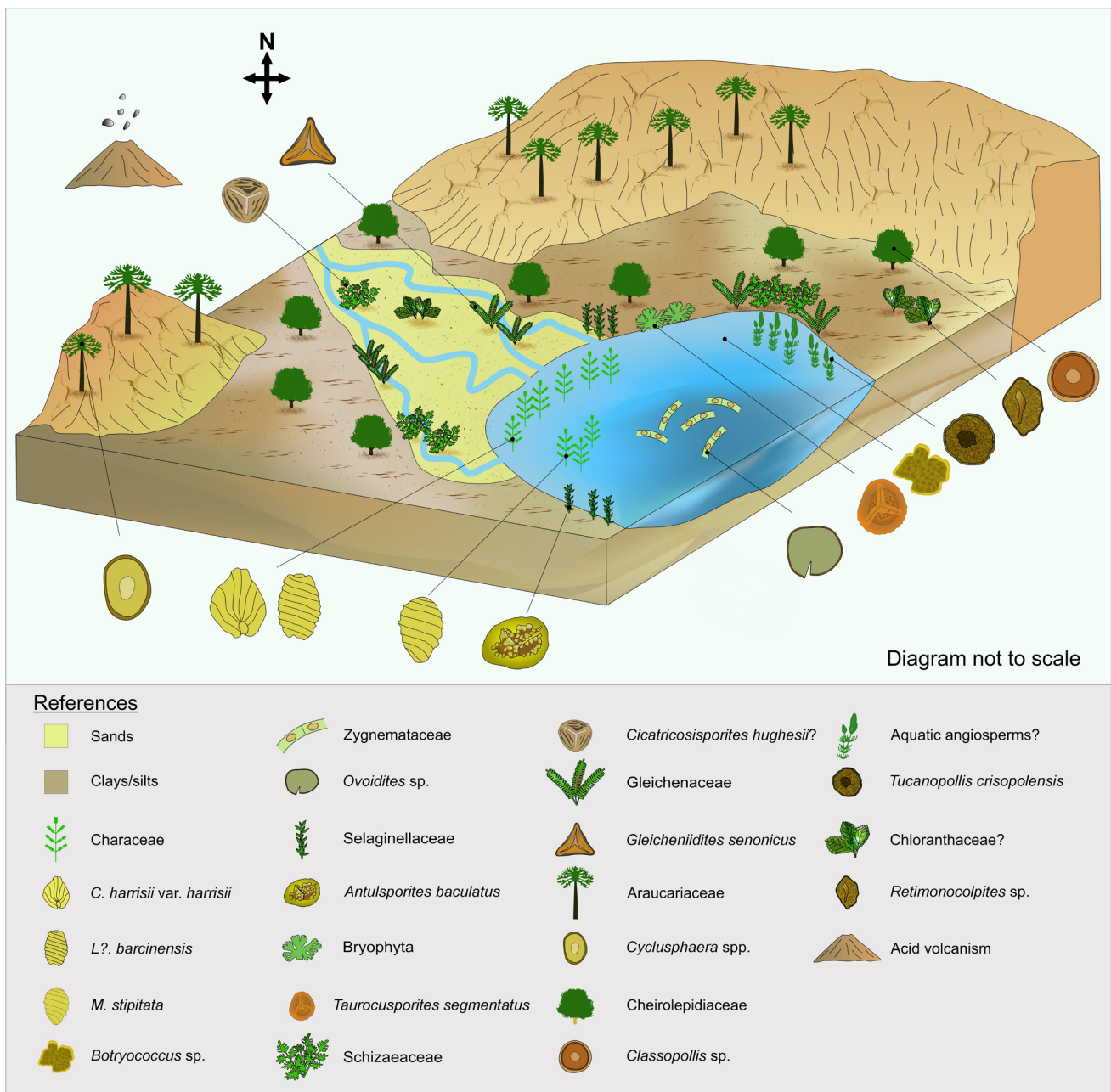


Figure 4. Paleoenvironmental reconstruction of the Pozo D-129 Formation at Sierra Silva, based on the analysis of charophytes and palynomorphs. The topographically elevated areas may correspond either to Paleozoic igneous-metamorphic basement rocks or to volcanic units of the Bahía Laura Volcanic Complex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

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).

In particular, 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 agree 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).

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 Salviniiales, 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 geiseltensis* (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.

It is worth noting that Gamero (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).

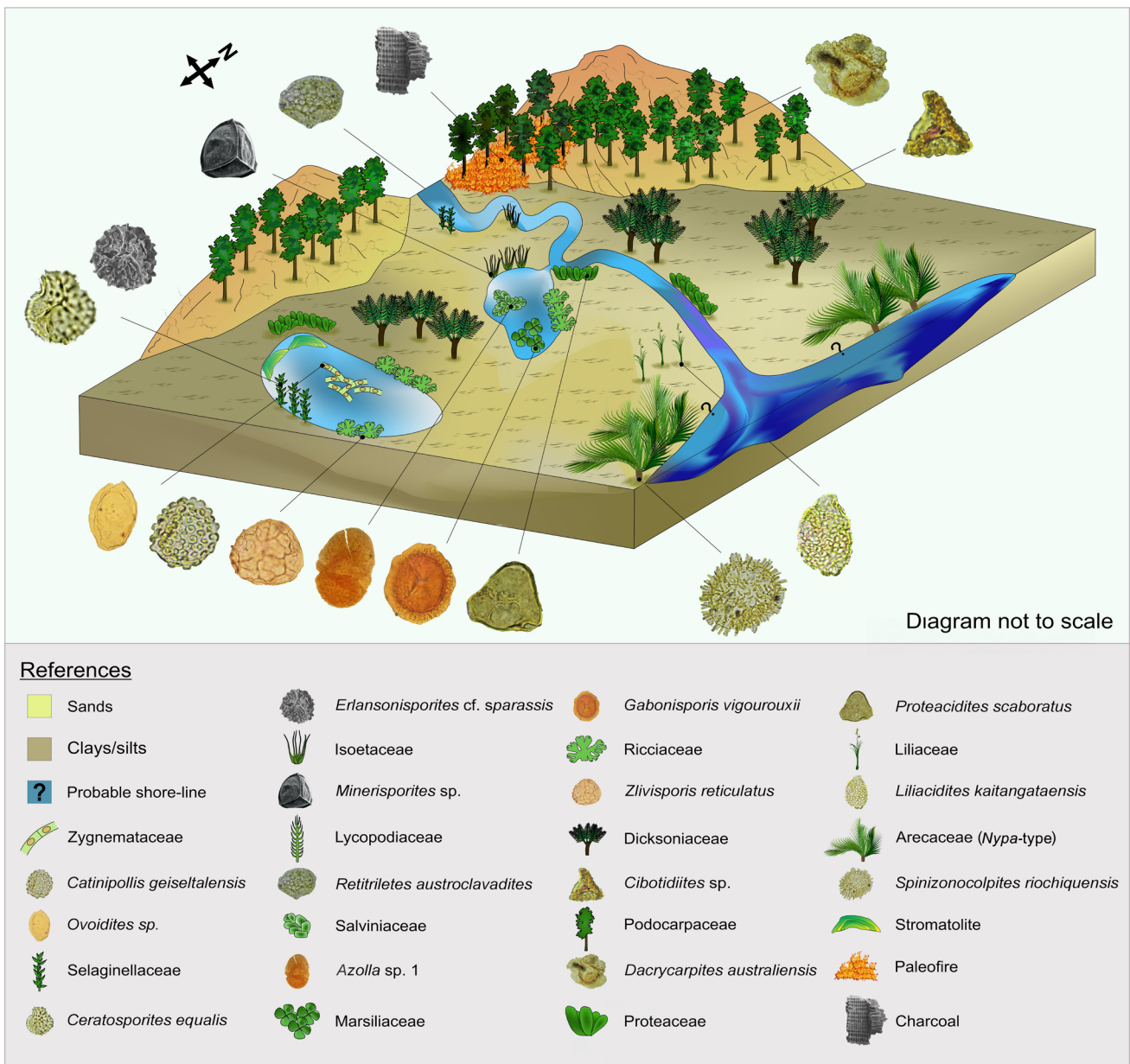


Figure 5. Paleoenvironmental reconstruction of the Lago Colhué Huapi Formation at the headwaters of the Río Chico, based on the analysis of palynomorphs and megaspores (modified from Vallati *et al.*, 2020). The topographically elevated areas are likely associated with previously deposited rocks of the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

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 (Vallati *et al.*, 2020 and references therein).

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 recognition 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).

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.

Acknowledgments. We acknowledge Dr. José Paredes for inviting us to participate with this review paper. The authors also wish to thank Dr. César Navarrete for interesting discussions on geological aspects of the basin. We also want to thank the reviewer Magdalena Llorens as well as the editor José Paredes whose suggestions and comments improve the original manuscript during the peer review process.

REFERENCES

- Allard, J., Foix, N., Buetti, S., Sánchez, F., Ferreira, L. and Atencio, M. (2020). Comparative structural analysis of inverted structures in the San Bernardo fold belt (Golfo San Jorge basin, Argentina): Inversion controls and tectosedimentary context of the Chubut Group. *Journal of South American Earth Sciences*, 97, 102405. <https://doi.org/10.1016/j.jsames.2019.102405>
- Archangelsky, S., Baldoni, A., Gamero, J. C. and Seiler, J. (1984). Palinología estratigráfica del Cretácico de Argentina austral III. Distribución de las especies y conclusiones. *Ameghiniana*, 21, 15–33. <https://www.ameghiniana.org.ar/index.php/ameghiniana/article/view/1726>
- Archangelsky, S., Bellosi, E. S., Jalfin, G. A. and Perrot, C. (1994). Palynology and alluvial facies from the mid-Cretaceous of Patagonia, subsurface of San Jorge Basin, Argentina. *Cretaceous Research*, 15, 127–142. <https://doi.org/10.1006/cre.1994.1006>
- Barreda, V., Bellosi, E. S. and Jalfin, G. (2003). *Celyphus rallus* Batten en depocentros del Cretácico Temprano, flanco norte de la Cuenca San Jorge: significado estratigráfico y oleogenético. *Revista del Museo Argentino de Ciencias Naturales, Nueva Serie* 5, 215–224. <http://revista.macn.gov.ar/ojs/index.php/RevMus/article/view/50/45>
- Bowman, V., Francis, J. E., Askin, R., Riding, J. B. and Swindles, G. T. (2014). Latest Cretaceous–earliest Paleogene vegetation and climate change at the high southern latitudes: palynological evidence from Seymour Island, Antarctic Peninsula. *Palaeogeography Palaeoclimatology and Palaeoecology*, 408, 26–47. <https://doi.org/10.1016/j.palaeo.2014.04.018>
- Carignano, A. P., Paredes, J. M., Olazábal, S. X. and Valle, M. N. (2017). Ostracoda (Crustacea) from the Pozo D-129 Formation (upper Barremian?–Aptian), Golfo San Jorge Basin, Patagonia, Argentina: Taxonomic descriptions, paleoenvironments and palaeogeographical implications. *Cretaceous Research*, 78, 206–220. <https://doi.org/10.1016/j.cretres.2017.06.015>
- Casal, G. A., Vallati, P., Ibiricu, L. M., De Sosa Tomas, A., Foix, N., Allard, J. O. and Martínez, R. D. (2020). Primer registro de estromatolitos en el Maastrichtiano tardío del Grupo Chubut, Cuenca del Golfo

- San Jorge, Patagonia central, Argentina. *Andean Geology*, 47, 162–178. <http://dx.doi.org/10.5027/andgeov47n1-3177>
- De Sosa Tomas, A., Vallati, P. and Martín-Closas, C. (2017). Biostratigraphy and biogeography of charophytes from the Cerro Barcino Formation (upper Aptian-lower Albian), Cañadón Asfalto Basin, central Patagonia, Argentina. *Cretaceous Research*, 79, 1–11. <https://doi.org/10.1016/j.cretres.2017.07.004>
- De Sosa Tomas, A., Martín-Closas, C. and Vallati, P. (2023). Charophytes from the Pozo D-129 Formation (lower Aptian, Lower Cretaceous), source rock in the Golfo San Jorge Basin, Patagonia, Argentina. *Cretaceous Research*, 151, 105652. <https://doi.org/10.1016/j.cretres.2023.105652>
- Doyle, J. A. and Endress, P. K. (2018). Phylogenetic Analyses of Cretaceous Fossils Related to Chloranthaceae and their Evolutionary Implications. *Botanical Review*, 84, 156–202. <https://doi.org/10.1007/s12229-018-9197-6>
- Friis, E. M., Pedersen, K. R. and Crane, P. R. (2010). Diversity in obscurity: fossil flowers and the early history of angiosperms. *Philosophical Transactions of the Royal Society B*, 365, 369–382. <https://doi.org/10.1098/rstb.2009.0227>
- Gamero, J. C. (1977). Megaspores del Cretácico de Patagonia III. Megaspores petrificadas del “Chubutense”, Prov. del Chubut, Argentina. *Ameghiniana*, 14, 100–116. <https://www.ameghiniana.org.ar/index.php/ameghiniana/article/view/1520>
- Harley, M. M. and Baker, W. J. (2001). Pollen aperture morphology in Arecaceae: application within phylogenetic analyses and a summary of the fossil record of palm-like pollen. *Grana*, 40, 45–77. <https://doi.org/10.1080/00173130152591877>
- Hechem, J., Figari, E. and Musacchio, E. A. (1987). Cuenca del Golfo San Jorge: Hallazgo de la Formación Pozo D-129. Información estratigráfica y paleontológica. *Petrotecnica*, 28(11), 13–15.
- Herngreen, G. F.W., Kedves, M., Rovnina, L. V. and Smirnova, S. B. (1996). Cretaceous palynofloral provinces: a review. In J. Jansonius and D. C. McGregor (Eds.), *Palynology: Principles and Applications*. American Association of Stratigraphic Palynologists Foundation, 3, 1157–1188.
- Kershaw, P. and Wagstaff, B. (2001). The southern conifer family Araucariaceae: history, status, and value for paleoenvironmental reconstruction. *Annual Review of Ecology, Evolution, and Systematics*, 32, 397–414. <https://doi.org/10.1146/annurev.ecolsys.32.081501.114059>
- Kvaček, J., Gomez, B. and Zetter, R. (2012). The early angiosperm *Pseudoasterophyllites cretaceus* from Albian–Cenomanian of Czech Republic and France revisited. *Acta Palaeontologica Polonica*, 57(2), 437–443. <https://doi.org/10.4202/app.2009.0060>
- Lamont, B. B. and He, T. (2012). Fire-adapted Gondwanan Angiosperm floras evolved in the Cretaceous. *BioMed Central Evolutionary Biology*, 12, 223. <https://doi.org/10.1186/1471-2148-12-223>
- Lamont, B. B., He, T., Milne, L. A. and Cowling, R. M. (2024). Out of Africa: Linked continents, overland migration and differential survival explain abundance of Proteaceae in Australia. *Perspectives in Plant Ecology, Evolution and Systematics*, 62, 125778. <https://doi.org/10.1016/j.ppees.2024.125778>
- Miller, M. and Marino, J. (2019). New insights from the Neocomian basins in the West of Chubut and Santa Cruz provinces, Argentina. *Journal of South American Earth Sciences*, 96, 102255. <https://doi.org/10.1016/j.jsames.2019.102255>
- Navarrete, C. R., Gianni, G. M. and Folguera, A. (2015). Tectonic inversion events in the western San Jorge Gulf Basin from seismic, borehole and field data. *Journal of South American Earth Sciences*, 64, 486–497. <https://doi.org/10.1016/j.jsames.2015.09.012>
- Paredes, J. M., Foix, N. and Allard, J. O. (2016). Sedimentology and alluvial architecture of the Bajo Barreal Formation (Upper Cretaceous) in the Golfo San Jorge Basin: Outcrop analogues of the richest oil-bearing fluvial succession in Argentina. *Marine and Petroleum Geology*, 72, 317–335. <https://doi.org/10.1016/j.marpetgeo.2016.02.013>
- Pérez Loinaze, V., Césari, S.N., Giordano, S.R., and Stach, N.H. (2019). Palynological analysis of a Lower Cretaceous subsurface succession from the south flank of the Golfo San Jorge Basin, Argentina. *Cretaceous Research*, 97: 94–106.
- Pérez Loinaze, V., Giordano, S.R., and Limarino, C.O. (2021). Late Cretaceous palynomorphs from the Golfo San Jorge Basin, Argentina. *Journal of South American Earth Sciences*, 107: 103151.
- Pérez-Cano, J., Bover-Arnal, T. and Martín-Closas, C. (2022). Charophyte communities in Barremian Iberian wetlands. *Facies*, 68, 13. <https://doi.org/10.1007/s10347-022-00651-6>
- Pérez-Cano, J., Pereira, H. J. R., Mendes, M., Pereira, Z., Callapez, P. M. and Fernandes, P. (2023). Upper Barremian–lower Aptian charophyte biostratigraphy from Arrifes section (Algarve Basin, Southern Portugal): correlation with dinoflagellate cyst biostratigraphy. *Cretaceous Research*, 150, 105575. <https://doi.org/10.1016/j.cretres.2023.105575>
- Soulié-Marsche, I. (2008). Charophytes, indicators for low salinity phases in North African sebkhet. *Journal of African Earth Sciences*, 51, 69–76. <https://doi.org/10.1016/j.jafrearsci.2007.12.002>
- Vajda, V. and Bercovici, A. (2012). Pollen and Spore stratigraphy of the Cretaceous–Paleogene Southern Hemisphere. *Journal of Stratigraphy*, 36(2), 153–164.
- Vallati, P. (1996). *Palynology of the D-129 Formation in the San Jorge Gulf Basin, Lower Cretaceous, Patagonia, Argentina* [Abstract]. 39° Congreso Brasileiro de Geologia, Salvador, Brasil.
- Vallati, P. (2013). A mid Cretaceous palynoflora with *Tucanopollis crisopolensis* from Pozo D-129 Formation, Golfo San Jorge Basin, Argentina. *Revista Brasileira de Paleontologia*, 16, 237–244. doi: 10.4072/rbp.2013.2.06
- Vallati, P., Casal, G., Foix, N., Allard, J., De Sosa Tomas, A. and Calo, M. (2016). First report of a Maastrichtian palynoflora from the Golfo San Jorge Basin, central Patagonia, Argentina. *Ameghiniana*, 53, 495–505. <https://doi.org/10.5710/AMGH.28.12.2015.2948>
- Vallati, P., De Sosa Tomas, A., Casal, G. and Calo, M. (2017). Salviales from the Late Cretaceous of the Golfo San Jorge Basin. *Cretaceous Research*, 74, 45–55. <https://doi.org/10.1016/j.cretres.2017.02.004>
- Vallati, P., De Sosa Tomas, A. and Casal, G. (2018). *Charcoalified plant remains from the Golfo San Jorge Basin, Argentina: evidence of wildfire during the Late Cretaceous* [Abstract]. 1° Palaeontological Virtual Congress.
- Vallati, P., De Sosa Tomas, A. and Casal, G. A. (2020). A Maastrichtian terrestrial palaeoenvironment close to the K/Pg boundary in the Golfo San Jorge Basin, Patagonia, Argentina. *Journal of South American Earth Sciences*, 97, 102401. <https://doi.org/10.1016/j.jsames.2019.102401>
- Van Nieuwenhuise, D. S. and Ormiston, A. R. (1989). *A model for the origin of source-rich lacustrine facies, San Jorge Basin, Argentina* [Abstract]. 1° Congreso Nacional de Exploración de Hidrocarburos, Mar del Plata, Argentina.
- Volkheimer, W. (1980). *Microfloras del Jurásico Superior y Cretácico Inferior de América Latina* [Abstract]. 2° Congreso Argentino de Paleontología y Bioestratigrafía y 1° Congreso Latinoamericano de Paleontología, Buenos Aires, Argentina.