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PALYNOLOGICAL, MEGAFLOREAL AND MESOFOSSIL RECORD FROM THE BAJO GRANDE AREA (ANFITEATRO DE TICÓ FORMATION, BAQUERÓ GROUP, UPPER APTIAN), PATAGONIA, ARGENTINA

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ABSTRACT.

The late Aptian flora of Baqueró is one of the best known and accurately dated Cretaceous plant associations from Gondwana, recognized for their well-preserved fossil remains. The Cerro Bayo (Bajo Grande area, Argentinean Patagonia) is one of its classical locations and includes the northernmost fossiliferous outcrops of the Baqueró Group, which belong to the Anfiteatro de Ticó Formation. It yields diverse and numerous plant megafossils and reproductive structures with associated pollen. We report a complete systematic study of a palynological association with 124 species, including 26 that are identified for the first time in the unit. This allowed the first record of three major botanical groups not reported before (i.e. lycophytes, hornworts and angiosperms), as well as algae and fungal spores. The same

fossiliferous levels also yielded megafossil remains and the first record of a mesofossil assemblage for the Baqueró flora. By integrating all these floristic data sources, relative abundance analyses, and sedimentological data it is possible to propose a palaeoenvironmental reconstruction of the Bajo Grande area during the late Aptian: a diverse forest growing in a temperate to warm climate with subtle variations between those associations from floodplains with water instability within a delta and those that grew into a more stable area out of the flooding influence. Thus, the presumed xeromorphic features identified in the Cerro Bayo flora (sunken stomata, papillae, epicuticular waxes) may have been related to contemporaneous volcanic activity recorded in Patagonia rather than to dry conditions.

Keywords. PALYNOLOGY; MESOFOSSILS; PALAEOFLORA; APTIAN; PATAGONIA

1. Introduction

The Baqueró Group is widely known for its fossil flora, in particular for the diversity and preservation quality of the contained plants. The age of this Group is also crucial. Precisely dated as late Aptian (Césari et al., 2011, Perez Loinaze et al., 2013, Passalia et al., 2016), its deposition temporally overlaps with an important event in plant evolution at middle palaeolatitudes: the earliest diversification of flowering plants. Baqueroan palaeofloras were exposed to environmental conditions that were recurrently stressful owing to persistent and increasing volcanic activity. Thus, it provides an opportunity to correlate morphological and anatomical features with environmental parameters (Archangelsky and Taylor, 1986).

Bajo Grande is the northernmost fossiliferous area hosting Baqueró Group exposures and is considered one of the classical fossiliferous localities of the “Baqueró Flora”. In fact, outcrops located at Bajo Grande include some of the most abundant and exquisitely preserved

fossils recorded from the Baqueró Group (Archangelsky, 1966, 1967, 1968, Traverso, 1968; Archangelsky and Baldoni, 1972a, 1972b, Baldoni, 1974, Archangelsky and Taylor, 1986, Del Fueyo, 1991, Artabe, 1994, Villar de Seoane, 1996, 1997, 1999, 2005, Archangelsky and Villar de Seoane, 2004, Cladera et al., 2007, Passalia et al., 2010, Vera and Césari, 2015). Rarely preserved plant organs have been recovered from this locality, such as thalloid liverworts [*Ricciopsis grandensis* (Cladera et al. 2007)], and fertile structures found isolated (Archangelsky and Villar de Seoane, 2004) or in organic connection with vegetative parts (Archangelsky, 1968, Cladera et al., 2007). Moreover, reproductive structures of six gymnosperm taxa with *in situ* pollen have been described (Archangelsky, 1966, Gamero, 1965, 1968, Archangelsky and Gamero, 1968, Del Fueyo, 1991, Archangelsky and Villar de Seoane, 2004). On the other hand, palynological assemblages have not been studied at this locality until the work of Passalia et al. (2016).

The Bajo Grande area is not only important for its fossil plants. It is also one of the few sites where Baqueró Group outcrops have yielded information on other elements of the late Aptian palaeobiota, including epiphyllous fungi (recognized by four microthyrial membranous thyrithocia (Marquez, 1968), and two fossil insects: a cockroach (Pinto, 1990) and a dragonfly (Petrulevicus and Nel, 2003). Recently, Passalia et al. (2016) clarified the stratigraphy, position of the fossiliferous levels, and provided a new absolute age for the Bajo Tigre Formation of the Baqueró Group.

This study presents a detailed palynological analysis of the Anfiteatro de Ticó Formation in the Bajo Grande area, and integrates for the first time the palynological results with the megafloreal record and new mesofossil data, in order to provide a complete overview of the region's Aptian flora. We compare the sedimentological features with the palaeobotanical data in order to better interpret the palaeoenvironment of the area.

2. Geological setting

The Baqueró Formation, defined by Archangelsky (1967) was raised to the rank of Group and divided into three formations (i.e. the Anfiteatro de Ticó, Bajo Tigre and Punta del Barco, in ascending stratigraphic order) by Cladera et al. (2002). This unit crops out in the Macizo del Deseado area (Santa Cruz Province) and is very well exposed in the Bajo Grande area, especially at the Cerro Bayo locality (Fig. 1).

FIGURE 1

Although Cerro Bayo has been the focus of numerous studies, a detailed stratigraphic framework was lacking, resulting in some inconsistencies in the stratigraphic subdivision of the succession (Archangelsky, 1967, Hechem and Homoc, 1987, Cladera et al., 2007). One of the most conspicuous discrepancies was the correlation of the upper part of the exposed section. Archangelsky (1967) and Cladera et al. (2007) considered it to be part of the upper section of the Baqueró Group, whereas Hechem and Homoc (1987) interpreted it as corresponding to the Laguna Palacios Formation, the uppermost unit of the Chubut Group. Recently, Passalia et al. (2015) undertook a detailed stratigraphic and environmental analysis of the succession, and registered an accurate date for the upper section of 116.85 ± 0.26 Ma. Thus, correlation with the Chubut Group was discarded, given that the age is coherent with that of the Bajo Tigre Formation, the middle unit of the Baqueró Group, and is temporally bracketed by the underlying Anfiteatro de Ticó Formation (118.23 ± 0.09 Ma, Pérez Loinaze et al., 2013) and overlying Punta del Barco Formation (114.67 ± 0.18 Ma, Césari et al., 2011). Based on these ages, it was suggested that the entire Baqueró Group was deposited during the late Aptian. However, Passalia et al. (2017) identified an assemblage of putative basal eudicots (*aff.* Ranunculales) from the uppermost levels of the Punta del Barco Formation, and

suggested that the youngest levels of the Baqueró Group may have been deposited during the earliest Albian.

Passalia et al. (2016) characterized the palaeoenvironmental evolution of the Baqueró Group in the area in terms of three facies associations. The lower facies association represents marginal lacustrine deposits, and is separated from the middle facies association by a flooding surface, which marks an expansion of the lake system. Finally, the upper facies association corresponds to a strong change in the environmental conditions, since the lacustrine system was rapidly shallowed by a large influx of pyroclastic material. The lower facies association *sensu* Passalia et al. (2016) is 40 m thick, and incorporates two types of fine-grained sediments, which are associated with conglomerates, deposited in a Gilbert-type delta system. Laminated mudstones and carbonaceous shales were deposited in subaerial interchannel areas of the delta. The second type consists of muddy and tuffaceous shallow lacustrine facies with reduced organic matter content that pass laterally into the Gilbert-type delta deposits. Five palynological samples were recovered from these fine-grained rocks at three productive levels (Fig. II).

FIGURE II

3. Palaeobotanical background

The knowledge of the palaeobotanical content of the Anfiteatro de Ticó Formation at Cerro Bayo begins with Archangelsky (1966) and includes many later studies whose results are detailed below. The fossil findings from Cerro Bayo have been historically referred to two stratigraphic levels identified as “NF *Araucarites*+NF II” adding later a third level, here mentioned as “levee level” (see Table III). The main megafloreal remains are related to gymnosperm taxa, mostly consisting of conifers, bennettites and cycads, but also including an ephedralean and a putative pteridosperm. Cycadales are represented by abundant sterile and

fertile organs without accurate affinities (Archangelsky and Baldoni, 1972, Baldoni, 1974; Villar de Seoane, 1997), and a zamiaceous leaf compression with well-preserved cuticle (*Restrepophyllum chiguoides* Passalia et al., 2010). On the other hand, Bennettitales are widely represented at this locality, where ten leaf species have been described (Archangelsky, 1966, Archangelsky and Baldoni, 1972, Villar de Seoane, 1997, 2005, Archangelsky and Villar de Seoane, 2004).

Among conifers, representatives of Araucariaceae, Cheirolepidiaceae and Podocarpaceae have been identified, in addition to four taxa of uncertain affinities (Archangelsky, 1966, Traverso, 1968, Archangelsky and Taylor, 1986, Del Fueyo, 1991, Passalia et al., 2016) (Table III). Leafy shoots with scale-like leaves are frequently found in Mesozoic strata, but establishing affinities is often difficult because of this leaf type is widely present within conifers. Noteworthy, at Cerro Bayo, some leaf-bearing branches have been found in organic connection with male cones containing pollen grains, allowing the conclusive referral to certain families.

Araucariaceae is represented in this locality by three taxa. One of them, *Notopehuén brevis*, consists of *Brachyphyllum*-bearing branches organically attached to male cones containing *Araucariacites*-type pollen grains (Del Fueyo, 1991). The other two consist of isolated ovuliferous bract-scales complexes referred to *Araucarites* (Archangelsky, 1966).

Podocarpaceae is recognized by the presence of the leafy branches *Apterocladus lanceolatus* with male cones in organic connection, from where *Callialasporites* pollen was recovered (Archangelsky, 1966, Gamero, 1965).

The *Classopollis* pollen grain is a diagnostic element to recognize Cheirolepidiaceae. Some twigs of *Tomaxellia biforme* Archangelsky were found attached to female cones, and male cones with *in situ* *Classopollis* pollen (Archangelsky, 1966, 1968, Archangelsky and Gamero, 1967). More recently, Passalia, et al. (2016) reported the first anatomically

preserved wood fragments at the locality, referred to *Brachyoxylon baqueroensis* Vera and Césari, probably also related to this family. Based on their cuticular features (see supplementary material I) the sterile branches of *Brachyphyllum baqueroense* Traverso may represent another cheirolepidaceous taxa.

Although quite diverse during the Mesozoic and well-represented in the palynological content, ferns are not abundant in the Cerro Bayo megaflorestic assemblage. Representatives of Cyatheaceae (*Cyathea cyathifolia*, Villar de Seoane, 1996, 1999), Schizaeaceae (Schizaeaceae *incertae sedis*, Cladera et al., 2007) and Pteridaceae (*Adiantopteris tripinnata*, Cladera et al., 2007) were identified (Table III).

The palaeofloristic association is completed with four species of *Sphenopteris*, the putative pteridosperm *Pachypteris elegans*, and the ephedralean *Ephedra verticillata*. Until now, angiosperms were not recorded in the macroflora of Cerro Bayo (Table III).

4. Materials and Methods

The studied locality, known as Cerro Bayo (47° 47' 31.7''S 68° 45' 22.4''W), is located at the Bajo Grande area, north-center of Santa Cruz Province, Argentina (Fig.I). Five fertile samples were collected at this area from the Anfiteatro de Ticó Formation (BA Pal 6386–6390). These were obtained from three stratigraphical levels (L1–L3) that belong to the lower facies association *sensu* Passalia et al. (2016) (Fig. II). The samples were treated by means of standard techniques for extraction and concentration of palynomorphs (Phipps and Playford, 1984). Observations were made with an Olympus BX-51 microscope equipped with a Nikon DS-Fi1 digital camera for photomicrography. Coordinates of the illustrated specimens are cited as England Finder references.

Among the preserved organic matter, important components were fragments of leaf cuticles, here grouped in informal morphotypes (CBY). Given the fragmentary nature of these remains, the conclusive referral to a particular taxon is problematic. However, a probable taxonomic placement or affinity is included, based in comparisons with the well-known record of impression/compression leaves with preserved cuticles known from Anfiteatro de Ticó Formation at Cerro Bayo and other localities.

The slides are deposited in the Palynological Collection of the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (BA Pal), under the numbers 6386–6390. For each sample, a total of at least 300 palynomorphs were counted to estimate the relative abundance of each taxon or plant group. This was done on one or two slides for each sample, depending on the palynomorph abundance. From counts of specimens by taxon, the following relative abundance categories have been established: rare (up to 5), common (6 to 10), frequent (11 to 15), abundant (16 to 25) and very abundant (more than 25). The relative percentages of the taxa were also calculated. Graphic representation of the quantitative distribution of palynomorph groups was made using Tilia 2.0.41 (Grimm, 1994–2015).

The suprageneric classification scheme used in this work follows the recent proposals of Chase and Reveal (2009) and Christenhusz et al. (2011a, b).

5. Results

5.1 Palynological record

Although the megafloristic record here reported for the Anfiteatro de Ticó Formation at the Cerro Bayo section is composed by taxa that have been already reported for the unit, the new palynological data notably increases the knowledge of the vegetation spectrum. Very well preserved palynomorphs were obtained from the five palynological samples recovered

from the three fertile stratigraphic levels (L1–L3) of the Anfiteatro de Ticó Formation at the Bajo Grande area (Fig. II).

A total of 124 taxa have been recorded, of which 73 are reported for first time at this locality, and 26 are new reports for the Anfiteatro de Ticó Formation. The palynological association is composed of 77 spore taxa and 39 pollen taxa, including four with angiosperm affinities. The assemblage is accompanied by freshwater algae (eight species) and fungi remains. Taxa identified in the study, along with their stratigraphic distribution and relative abundance is presented in Table I. The most unusual taxa, and those that have been recorded for the first time for the Anfiteatro de Ticó Formation, are illustrated in Plates I–II.

Twenty-one species (i.e. *Araucariacites spinosus*, *Capsispora vulcanica* and *Podocarpidites epistratus*) are only present in L1, mostly in low frequency. In addition, *Klukisporites* sp. is a very abundant taxon in this level (Table I). Fossiliferous levels L2 and L3 have only a few exclusive species. *Neveisporites similiscaris*, *N. vallatus*, *Leptolepidites proxigranulatus*, *Ruffordiaspora ludbrookiae* and *Perotrilites* sp. have been identified exclusively in L2, all as rare components except for the latter taxon, which is very abundant (Table I). On the other hand, *Cibotiumspora juncta*, *Distalanulisporites* sp. and *Peromonolites* sp. (Plate I) are abundant elements restricted to the L3.

Among the spore-producing plants, ferns reach from 6% to almost 38% of the total assemblage (Fig. III). Gleicheniaceae is present in all studied samples, with its higher abundances recorded in L1 (BA Pal 6390) and L2 (BA Pal 6388). Lower proportions of Schizaeaceae are observed in the three stratigraphic sections, as with Dicksoniaceae (*Cyatheacidites tectifera*). Other tree-ferns (Cibotiaceae and Cyatheaceae), may be present in the assemblage, represented by *Cyathidites* and *Cibotioidites*. However, affinities of these two fossil genera are unclear, and non-cyathealean ferns may produce similar spores (e.g. Balme, 1995). Osmundaceae, generally found in Mesozoic assemblages (e.g. Bomfleur et al., 2017,

Mays, 2015, Nagalingum et al., 2002), represent a minor proportion of the palynological samples, although being recovered from the three sections. Matoniaceae were a minor element of the assemblage (L1-L2), along with the water ferns Marsileaceae, the latter group being restricted to L1.

Spores of bryophytes and lycophytes are poorly represented or absent in some samples (Table I). They include representatives of the Bryophyta *sensu lato* (Marchantiidae and Anthocerotidae), showing low levels of abundance when present (up to 3.4%) (Fig. III). Lycopodiidae are represented by Lycopodiales and Selaginellales, and its greater abundance is recorded in sample BA Pal 6390 (2.1 %), having a lower degree of representation in the remaining samples.

In terms of relative abundance, the studied assemblages are dominated by gymnosperm pollen grains, reaching values between 61 and 97% (Fig. III). Among them, *Classopollis* (Cheirolepidiaceae) is the most abundant palynomorph in all the studied samples (between 25 and 84%), except in sample BA Pal 6390 (L1) in which *Cyclusphaera* pollen grains (Araucariaceae) dominates (Fig. III). Conifers are not only the most abundant plant group, but also the most diverse, with 28 species recognized in this study. The gymnosperm pollen spectrum includes also pollen grains of pteridosperms and ephedrales (Fig. III). Interestingly, distribution of those taxa is not homogeneous across samples (e.g. Araucariaceae in L1 and L2; Podocarpaceae in L1) (Fig. III). Bisaccate and trisaccate pollen grains of Podocarpaceae are also common, and have highly variable percentages, ranging between 4 and 32% of the total assemblage.

Cycadopites follicularis, which may be related to Ginkgoales, Cycadales, Bennettitales, Pentoxylales or Pteridospermales is present in very low proportions in the three stratigraphic sections. Its scarcity may be related to a real low abundance of parent plants, or may be to the delicate nature of the pollen wall (e.g. Archangelsky and Villar de Seoane, 2004).

Furthermore, some of these clades have been recognized as having entomophilous dispersion mechanisms (e.g. Peñalver et al., 2015), resulting in lower production of pollen grains.

Pteridosperms (e.g. *Vitreisporites* spp.) were recorded in all studied samples, although with low diversity and abundance (Table I). A scarcer element in the assemblage are ephedrales (Ephedripites *multicostatus*), identified only in sample BA Pal 6386.

Angiosperms are represented by *Clavatipollenites* spp., cf. *Jusinghipollis ticoensis* Llorens and Perez Loinaze, and *Lethomasites* sp. *Lethomasites* is a genus often considered as having angiosperm affinities. Some authors have suggested that it has affinities with Magnoliales (i.e. Annonaceae, Degeneriaceae, Magnoliaceae, Eupomatiaceae, Himantandraceae, and Myristicaceae), although none of the extant taxa has pollen grains with all the characteristics observed in this fossil type (Doyle and Hotton, 1991, Ward et al., 1989). In addition, *Lethomasites* has some features also present in the bennettitalean lineage (Crepet and Nixon, 1994).

Angiosperms, a clearly minoritarian element in the assemblage, is recognized in most of the samples. This group is common in L1 (only recorded in the counting at this level) and a very rare element in L2 and L3.

Algae are present in very low proportions in L1 and L2, comprising less than 1% of the total assemblage identified in the sample BA Pal 6386, and not being recorded in the counts of L2, or in the sample BA Pal 6390 of L1, and absent at L3.

In the analysis of species diversity of the association, in general terms, the spore-producing plants represent 62% of the total species richness, while 31.45% correspond to spermatophytes, and 6.45% to freshwater algae. Regarding spermatophytes, the most diverse group are by far the conifers, representing 23% of the total species diversity. Pteridosperms, flowering plants and *incertae sedis* taxa are, as whole, minor elements of the assemblage,

reaching 2.4% each one, while ephedrales only represent 0.8%. Finally, 6.4% of the recognized taxa correspond to cysts of freshwater algae.

In summary, the palynological composition reveals the presence of several spore-bearing taxa (ferns, lycopsids and bryophytes), conifers, pteridosperms, ephedrales and angiosperms, along with freshwater algae and fungi, and some taxa of uncertain affinity.

5.2 Messofofossils

5.2.1. Isolated cuticles

Well-preserved cuticle remains are present across the three fossiliferous levels. They comprise 45–80 % of the palynological residue in samples BA Pal 6386 (L1), 6387 (L2) and 6389 (L3). At least eleven cuticle morphotypes have been identified, including bennettites, conifers and a putative pteridosperm. They are listed in Table II, illustrated in Plates III–IV, and described in detail in the supplementary material I. Distribution of cuticle morphotypes is not homogeneous across the three fossiliferous levels. As with the study of spores and pollen grains, the only observable differences are between the L3, where all the morphotypes identified are present, and the other two levels. Bennettitales that were not conclusively recorded in the pollen assemblage were identified by cuticular remains. Seven cuticle types are referable to papillate and non-papillate bennettites (CBY-1 to CBY-7). Three cuticle types of conifers were also identified, one of them resembling the Cheirolepidiaceae *Tomaxellia degiustoi* (CBY-11), other representing the putative Cheirolepidiaceae *Brachyphyllum baqueroense* (CBY-8) whereas the third cuticle type (CBY-10) has traits observed in *Brachyphyllum* spp. from the Baqueró Group, but precluding its assignment to one or another family and even probably including more than one conifer species. A pteridosperm (CBY-9) was presumably identified in L3, represented by cuticle fragments with traits like

those of some species of the putative pteridosperm *Rufloiria*. No cuticles referable to angiosperms or spore-bearing taxa were found in the assemblages. Taken as a whole, the floral assemblage revealed from the cuticular remains consists of a diverse array of bennettites, along with conifers, including Cheirolepidiaceae, and other *incertae sedis* spermatophytes having minor representation.

TABLE II

5.2.2. Fungal remains

Fungal mesofossils related to Microthyriaceae were identified in sample BA Pal 6389 (L3). They consist of epiphyllous stroma remains, extremely thin and relatively large, circular to irregular in shape, with a lobed or denticulate rim (Plate IV.6). They are referable to *Brefeldiellites argentina*, a taxon described previously from this locality (Martinez, 1968). In addition, at least four types of disperse fungal spores (Plate II.15–16) were identified, recovered from the three stratigraphic levels.

5.2.3. Wood remains

Wood remains were obtained from L1. They were studied under SEM because petrographic cross-sections were unsuccessful due to preservation issues. Thus, percentages of types of pits in the radial walls were impossible to calculate. Radial walls of the tracheids bear circular bordered pits, arranged in uniseriate, mostly araucarioid pattern, but also in abietinoid patterns. Cross-fields are araucarioid, bearing 4–11 cupressoid pits, and rays are uniseriate, 4–8 cells high (Plate IV.9–11). These features are comparable to *Agathoxylon* and *Brachyoxylon*. In particular, observed features are shared with *Brachyoxylon baqueroensis* Vera and Césari 2015, found in the Anfiteatro de Ticó and Punta del Barco Formations.

Given the stratigraphic relationship and similar features, the remains here studied are assigned to this species.

PLATES III–IV

5.3 Megafloreal remains

Megafloreal remains were recovered from L1 and L3 levels, and were illustrated in Passalia et al. (2016). Those materials, along with previously published records, and complete stratigraphic distribution, are listed in Table III. Gymnosperms are proportionately more abundant and diverse than spore-producing groups. Conifers are represented by three families (Araucariaceae, Cheirolepidiaceae and Podocarpaceae), along with taxa of uncertain affinities, having similar taxonomic composition in both stratigraphic levels. Cycadales are also recorded in both L1 and L3, with one species identified in L1 (*Sueria* sp.), which is also recorded along with *Ticoa lamellata* and *Pseudoctenis crassa* in L3. Among Bennettitales, five taxa were recorded, two of them present in both stratigraphic levels, one exclusive to L1, and other two exclusive to L3. In addition, a single record of a putative unkomasialean sterile leaf (*Pachypteris elegantis*) was recovered from the L1.

Among spore-producing taxa, only ferns of uncertain affinities were identified, with two taxa reported from the assemblage (*Cladophlebis antarctica* in L3, and indeterminate fern fronds from L1 and L3). In addition, two *Sphenopteris* species were identified in L3. This genus of unclear affinities may represent pteridosperms or other frond-bearing plant group. The palaeobotanical composition of both stratigraphic levels studied shows minor differences, as stated above: Cycadales seem to be slightly more diverse in L3; sphenopterid fronds are only found in L3; and *Pachypteris* is only identified in L1.

Previous megafloral records from this locality are not referred to the stratigraphic levels here recognized (L1 to L3) (Table III) due to the unclear stratigraphic relationships between them. Provenance of these taxa is identified as “NF *Araucarites*+NF II”, to indicate these two fossiliferous levels traditionally mentioned in the literature (see Archangelsky, 2003 and references there in, as well as Archangelsky and Villar de Seoane, 2004, Villar de Seoane, 2005). On the other hand, “levee level” is mentioned to indicate the provenance of the megafossils studied by Cladera et al (2007).

Encompassing the full megafloral record, this study added eight new taxa to the floristic association of the Bajo Grande area, including ferns (*Cladophlebis antarctica* (Nathorst) Halle and a pteridophyte indet.), cycads (*Zamiites* sp. and *Sueria* sp.), conifers (*Brachyphyllum* sp. and male cones indet.) (Table IV), and *incertae sedis* taxa [*Sphenopteris* (*Onychiopsis?*) *psilotoides* (Stokes and Webb) Ward and *Sphenopteris seriai* Archangelsky (1967b)]

TABLE III

6. Discussion

6.1. Integrated evidence

As was exposed above, the palynological and cuticle associations present a comparable pattern, where L1 and L2 are very similar in taxonomic content, and clearly different from what is recorded in L3. Contrasting, the megafloral record present in L1 and L3 shows few differences.

The composition of the flora is directly related to environmental and climatic changes in the area where the plants lived. Thus, plant megafossils, as well as palynomorphs and cuticle morphotype are good proxies for understanding climatic changes through time.

Usually, however, only one of these types of remains is used for reconstructions; the present study integrates all this information. It is interesting to note that each source of fossil data is more or less biased. Thus, some taxa almost unrecognized in some type of fossils (pollen grains and spores, cuticles or megafloreal remains) may be revealed when other fossil types are studied, a result probably related to their differences in taphonomic selection. For example, Cycadales and Bennettiales are almost absent in the pollen record but are revealed as having comparatively high diversity in the cuticular and megafloreal record as well. As a result, to have a representative picture of the palaeoflora recorded in the Anfiteatro de Ticó Formation at Cerro Bayo, the data obtained from the three sources (5.1 to 5.3) is qualitatively integrated and discussed.

The palynological assemblages of Cerro Bayo presents the most comprehensive record, comprising groups of non-vascular and spore-bearing plants, algae, fungi and spermatophytes (including angiosperms). Two types of sources can be recognized in this palynological record. One of them represents the regional vegetation, which corresponds mainly to anemophilous gymnosperm taxa; and the other represents local taxa, including spores (Moss et al., 2005) and angiosperms (Tosolini et al., 2018).

The megafloreal remains are a moderate record of the groups present, reporting the presence of non-vascular and spore bearing plants and the spermatophytes (excluding angiosperms). Nevertheless, it provides a more restricted view regarding the diversity of the groups, also excluding algae and fungi.

Finally, mesofossils proved to be the less comprehensive source, since they only reflect the presence of spermatophytes (excluding angiosperms) and fungi, while they overrepresent bennettites.

Spore bearing taxa were represented by several groups of plants. Non-vascular plants identified in the assemblage correspond to the Marchantiidae and Anthocerotidae, recorded as

isolated spores, along with the megafloral taxon *Ricciopsis grandensis* identified in the “levee level”. Lycopodiids are exclusively recorded in the spore record and allow the identification of Selaginellales and Lycopodiales. Among ferns, several groups are identified. Gleicheniaceae, Matoniaceae, Osmundaceae, Polypodiaceae, and Marsileaceae are part of the assemblage, exclusively represented by isolated spores. Schizaceae and Pteridaceae are observed in the spore record but are also tentatively identified as megafloral remains in the “levee level”. These groups probably represented the lower stratum of the community, or inhabited water bodies (Marsileaceae). The assemblage of ferns also incorporates representatives of the Cyatheales, as isolated spores (*Cyatheidites tectifera*, Dicksoniaceae) and megafloral remains previously reported from the “NF Araucarites+NF II” (*Cyathea cyathifolia*, Cyatheaceae), that may have been part of a higher stratum. Other fern groups could have been present, but their accurate affiliations are difficult to address (e.g. *Cladophlebis antarctica*, *Cyathidites* spp., *Cibotiidites*, *Perotrilites*, *Nevesisporites*).

Seed ferns were a minor but persistent group in the floral community and are represented by few pollen taxa (*Alisporites* and *Vitreisporites*), megafloral (*Pachypteris elegans*) and cuticle remains (CBY-9).

Cycadales and Bennettitales have similar representation in the flora. They are not conclusively recorded in the pollen assemblage (*Cycadopites follicularis* may be linked to these clades), but also with other groups of plants). This fact contrasts with their good representation in the meso and megafloral records. Cycadales includes three taxa recognized in this study (*Pseudoctenis crassa*, *Ticoa lamellata* and *Sueria* sp.). Furthermore, the number of cycads is increased to more than ten taxa if data from “NF Araucarites+NF II” is incorporated. Bennettitales also show high diversity, with several taxa reported in this work from the cuticular record (CBY-1 to CBY-7), and the megafloral remains (*Dictyozamites latifolius*, *Ptilophyllum antarcticum*, *P.* sp., *Zamites grandis* and *Z.* sp.). In addition, four

more taxa not recognized here were previously identified in “NF *Araucarites*+NF II” (Table III). Taken as a whole, Cycadales and Bennettitales seem to have been an important element in the floral assemblage.

Several conifer families are recognized in the studied sections, along with coniferous taxa of unknown affinities. Cheirolepidiaceae seem to have been one of the most abundant conifers in the area (and maybe one of the most abundant plant groups), judging by the pollen percentages (Fig. III). The taxonomy of *Classopollis* species is sometimes unclear, and many authors follow different criteria. Thus, the total number of species recorded in the studied pollen grains is difficult to determine, but it certainly is more than four taxa. In addition, cheirolepids are identified in the megafloreal record (*Tonaxellia biforme* and probably the wood *Brachyoxylon baqueroensis*) and the cuticle record (CBY-11 and probably CBY-8) (Tables II-III; Plate IV). The sterile twigs of *Tarphyderma glabra* and *Brachyphyllum baqueroense* (“NF *Araucarites*+NF II”), and more putative cheirolepids species to the Cerro Bayo flora. Araucariaceae are identified by several taxa in the palynological assemblages (*Cyclusphaera*, *Araucariacites* and *Eulneiopsis*), and megafloreal remains (*Notopheuen brevis* and two types of isolated bract-scale complex referred to *Araucarites*) (Table III). The third recognized family, Podocarpaceae, is present as a diverse array of pollen taxa (more than 18 species, Table I) and the megafloreal remains of *Apterocladus lanceolatus* and *Podocarpus dubius* (Table III). Other coniferalean records of unknown affinities are also presents (e.g. *Brachyphyllum*, CBY-10; Tables II-III; Plate IV).

Ephedrales are very minor element of the community, recorded scarcely by the pollen grain *Ephedripites multicostatus* (Table I), and by the megafloreal taxon *Ephedra verticillata* from the “levee level” (Table III).

Finally, as in other Patagonian floras of similar ages the angiosperms are scarcely represented, identified only by four taxa in the pollen assemblage (Fig. III, Table I).

Other remains recovered in the studied sections include algae, which probably inhabited small ponds and waterbodies (Table I) and fungi, represented by fungal spores and *Brefeldiellites argentina* Martinez 1968 (Fig. III, Table I).

6.2. Environments and climate

The facies associations recognized in the Anfiteatro de Ticó Formation, in various areas of the basin, indicate that it was deposited in fluvial sinuous channels associated to shallow and extensive lakes (i.e. Cladera et al., 2002, 2007, Limarino et al., 2012). At Bajo Grande area, the lower facies association described by Passalia et al. (2016) represents marginal lacustrine deposits. The plant bearing deposits consist of laminated mudstones that strongly suggest the existence of small deltas indicating the entrance of fluvial channels into a water body, within a low-energy flood basin. Interchannel areas in the subaerial platform of the delta bear abundant plant remains and charcofied wood.

The presence of water bodies, swamps or flooded areas in Cerro Bayo, as suggested by sedimentology (i.e. Cladera et al., 2007, Passalia et al., 2016), is confirmed by the record of algae such as *Botryococcus* sp., *Ovoidites* spp. and *Lecaniella* sp. *Botryococcus* sp. is a successful colonizer in shallow, alkaline water (e.g. inland saline lakes), with a wide range of climate conditions (Guy Ohlson, 1992; Zippi, 1998). The Zygnemataceae (*Ovoidites* spp., *Lecaniella* sp.), have modern representatives that develop in freshwater bodies, lakes, lagoons, marshes and slow currents, and their zygospores may require repeated drought conditions to initiate germination (Zippi, 1998). Interestingly, Zygnemataceae were recorded in L1 and L2, which belong to sediments deposited at a subaerial platform in the interchannel areas of a delta, characterized by unstable conditions, with alternating dry and wet periods. In addition, *Leiosphaeria*, a genus which has been referred to the Prasinophyta (Tappan, 1980, Guy-Ohlson, 1996), is recorded by two species, and is very abundant in L1 (BA Pal 6386).

The lithological evidences can be integrated with their palynological content, but for a detailed interpretation, a distinction must be made between the palynological record of local taxa (spores and angiosperms), over regional taxa (gymnosperm pollen, mainly conifers).

Thus, analyzing the local elements, the unstable niches, associated with the natural dynamics of the water bodies, could have been exploited by the angiosperms, as revealed by the presence of *Clavatipollenites* and cf. *Jusinghipollis ticoensis*. In fact, previous works suggests that many basal angiosperms were capable of colonizing disturbed environments including riverbanks, temporary ponds and periodically flooded plains (Retallack and Dilcher, 1981, Feild et al., 2004, Coiffard et al., 2006). Angiosperms are present at L1 and L2, and almost absent in L3. L1 also contains marsileaceous aquatic ferns. Contrasting, hydrophilic groups (e.g. algae, aquatic ferns) are absent in L3. In summary, the palynological associations studied in Cerro Bayo are quite similar, but present subtle differences between L1 and L2, which contain more elements of freshwater environments, with respect to L3 that almost does not present them. Therefore, this could suggest an environment without frequent flooding episodes during the L3 deposition.

The first palaeoclimatic estimates for the Baqueró Group were made by Archangelsky (1967) who based in the taxonomical composition, as well as by some morphological features recognized in the fossil plants, postulated prevailing temperate-moderate temperatures and moderately humid conditions, but probably alternating with relatively cold and dry periods, at least seasonally. Fossil conifer cuticles from the Anfiteatro de Ticó Formation at Cerro Bayo were included in a stomatal frequency analysis as atmospheric $p\text{CO}_2$ indicator (Passalia, 2009). This study revealed high $p\text{CO}_2$ values, coherent with temperate (cool) to warm climatic conditions for Patagonia. This latter result agrees with a gradual trend of warming in the South Atlantic sea-surface temperature since the late Aptian, as suggested by isotopic studies (e.g. Clarke and Jenkyns, 1999, Jenkyns et al., 2012).

Chaboureau et al. (2014) simulated biomes highlighting climate changes induced by palaeogeography, and suggested a temperate humid zone during the Aptian at the region where the Baqueró flora inhabited.

Based on their palynological content the Baqueró flora was included by Perez Loinaze and Llorens (2018) in the *Cyclusphaera psilata*-*Classopollis* Phytogeographic Subprovince (Volkheimer, 1980) of the Trisaccates Province (Herngreen et al., 1996), which is characterized by *Cyclusphaera* spp. and high percentages of *Classopollis* and *Callialasporites*. Palaeoclimatic signals may be discussed taking into account the Cerro Bayo assemblage composition, when some taxa are considered in the sense of nearest living relatives.

All palynological samples from the Anfiteatro de Ticó biota at Cerro Bayo show high percentages of *Classopollis* (Cheirolepidiaceae). According to Vakhrameev (1982, 1991), percentages of 60–90% of *Classopollis* indicate warm and dry conditions, and two of the five studied samples from Cerro Bayo fall within this range, whereas other two samples have slightly lower (but otherwise high values) representation of *Classopollis* (40–46%). However, the evidence set of this extinct group seems to indicate that it was adapted to a variety of climates and environments. It has been suggested that Cheirolepidiaceae were thermophilic and probably drought resistant shrubs and trees adapted to different arid environments, including specimens recorded in coastal and saline, but also associated with freshwater environments, as lakes and rivers (Alvin, 1982; Watson, 1988; Thévenard et al., 2005). Particularly for gondwanan palaeofloras, the presence of Cheirolepidiaceae has been associated to different environmental scenarios. For the records of *Classopollis* at northern Brazil it has been proposed that they inhabited nearby shorelines in a hot arid to semiarid climate (Herngreen, 1975, Lima 1976, Regali and Santos 1999) and, alternatively that they grew near the brackish environment of a hypothetical lagoon (Kunzmann et al., 2006). For

middle palaeolatitudes of South Africa, Scott (1976) reconstructed the coastal vegetation and included Cheirolepidiaceae as part of the assemblage. Moreover, in high palaeolatitudes, Antarctic cheirolepids would have grown under a humid temperate climate (Baldoni and Medina 1989). Finally, this family was widely distributed and grew in arid to humid climates in either continental or seashore environments, between 40° and 50°S palaeolatitudes (Del Fueyo et al., 2007; Del Fueyo and Archangelsky, 2010).

Other conifer groups recorded at Cerro Bayo are Podocarpaceae and Araucariaceae. Brodribb and Hill (2004) states that all extant podocarps exhibit quite low drought tolerance with broad-shoot genera particularly intolerant of drought. Similarly, extant broad-leaved South American podocarps also grow in wet environments (Donoso, 2013). Extant Araucariaceae are mostly restricted to the subtropics, extending into the marginal tropics (Kershaw and Wagstaff, 2001). Some exceptions include *Araucaria araucana* in southern regions of South America, which grows from warm-temperate to cold-temperate climates and tolerates important seasonal thermal amplitude (Donoso, 2013).

Ephedraceae is another element recognized in the Cerro Bayo flora (*Ephedripites multicostatus*, *Ephedra verticillata*). Extant Ephedraceae are xerophytic, growing in warm-temperate regions, and are in part cold-resistant (Kubitzky, 1990). According to Puebla et al. (2017) the co-occurrence of Ephedraceae associated with Cheirolepidiaceae suggests relatively seasonality.

Spore producing taxa are found in lower proportion when compared with pollen grains producers. Noteworthy, some spore producing plant groups are well-represented at the Cerro Bayo assemblage. The spores of marsileaceous ferns, lycophytes and bryophytes, are quite diverse and widely distributed but recorded in low percentages. These plants require hygrophilous wet habitats such as coastal swamps or ponds. Among this group, only liverworts are present in the megafloora.

The abundance of spores produced by ferns recorded in the studied assemblages is low to moderate. It might be indicative of a general lack of moist habitats suitable for this plant group. Nevertheless, it is interesting to note that most identified ferns (22 out of 34, excluding marsileaceous), corresponds to some groups linked to disturbed environments. Gleicheniaceae ferns are frequent in cretaceous ash beds, and are interpreted as important components of early successional vegetation (pioneer) after ash fall events (i.e. Crabtree, 1988), or fires (i.e. Herendeen and Skog, 1998). In the same way, Collinson (1996) suggested that many ferns of families such as Schizaeaceae, Gleicheniaceae and Dicksoniaceae were opportunists, colonizing open and disturbed grounds.

Fungal remains present in the Anfiteatro de Tico biota at Cerro Bayo consist of at least 4 types of disperse spores, and mesofossil remains related to Microthyriaceae, suggesting at least locally wet conditions. The distribution of extant Microthyriaceae is mostly restricted to tropics and subtropics, but they can be found, more rarely, in temperate and cold environments (Martínez, 1968). The palaeontological record of these epiphyllous fungi is generally associated with warm-temperate or subtropical vegetation (Dilcher, 1965, Conran et al., 2016).

A distinctive feature of the taphocenoses of Cerro Bayo is the presence of foliar cuticles preserved both, *in situ* over leaf compressions, as well as dispersed in palynological samples (the present work). In addition to its taxonomic information, some morphological features of the cuticles can be interpreted as palaeoenvironmental or palaeoclimatic indicators (e.g. Haworth and McElwain, 2008, and cites therein). However, it must be considered that a same cuticular feature may indicate adaptations to different environmental conditions which could be misinterpreted.

The preserved cuticles in Cerro Bayo assemblages belong mainly to cycads, bennettites and conifers. The development of a thick cuticle has usually been considered as

an adaptation to dry environmental conditions by reducing water loss via plant evapotranspiration (e.g. McElwain and Chaloner, 1996). However, Kerstiens (1996) and Riederer and Schreiber (2001) noted that cuticle thickness is not necessarily related to water loss resistance. Moreover, the cuticular membranes of Cerro Bayo plants have variable thickness and consequently its signal is at least ambiguous. For example, the cuticle thickness in cycads from Cerro Bayo ranges between 2–15 μm (Passalia et al., 2010). An outstanding feature of Cerro Bayo's cycads and bennettites is the presence of sunken stomata, in some cases with the development of relatively deep epistomatal chambers (e.g. *Mesosingeria oblonga*, *Ticoa lamellata*, *Otozamites parviauriculata*). Sunken stomata in these species are commonly surrounded, or their stomatal pore directly occluded, by papillae or trichomes, a feature observed in many of the dispersed cuticles (Table II; Plate IV). Conifers of Cerro Bayo also have somewhat sunken stomata and in one case (CBY-8 morphotype), with papilla covering the stomatal pore. An extreme morphological adaptation is present in *Tarphyderma glabra*. This conifer presents a thick cuticle (up to 15 μm) and guard cells deeply sunken in an elongated epistomatic chamber, which are partially obstructed by inner papillae disposed in their upper zone (Archangelsky and Taylor, 1986). Sunken stomata partially covered by papillae are commonly associated with leathery leaves, thick cuticles or papillate surfaces, and are often interpreted as xeromorphic anti-transpiring adaptations due to an increase in boundary layer resistance (Haworth and McElwain, 2008). However, these features not necessary are a response to a drought habitat, being that xeromorphism may also be caused by various other edaphic (nutrients, pH values and permeability of soils, salinity) or environmental factors (i.e. exposure to strong wind or excess of solar radiation) (e.g. Hill, 1998; Jordan et al., 2005; Pott et al., 2008, Steinhorsdottir et al., 2011, and cites therein).

Epicuticular waxes have been recognized in the cuticular surface of some species from Cerro Bayo (Archangelsky and Taylor, 1986; Passalia et al., 2010). Reduction of water

permeability across the cuticle would seem to be the primary function of epicuticular waxes (Schönherr, 1982), an evident advantage in dry and/or warm conditions. However, it has been suggested that two-level hierarchical surface structuring formed by papillose cell sculptures with smaller superimposed three-dimensional waxes, produces on the plant surface a superhydrophobic effect that allows to prevent the formation of water films, which reduces the gas exchange dramatically and promotes the formation of pathogenic microorganisms (biofilms) (Koch and Barthlott, 2009, and cites therein). Consequently, it would be advantageous for plants growing in humid environments. On the other hand, the self-cleaning of plant surfaces by water repellence is a protection against particle accumulation (Koch and Barthlott, 2009) as caused by recurrent ash fall. The presumed xeromorphic features identified in the Cerro Bayo flora (sunken stomata, papillae, epicuticular waxes) may have been related to the volcanic activity recorded in Patagonia at that time, rather than dry environmental conditions (Archangelsky and Taylor, 1986). The presence of accessible moisture sources for the flora of the Baqueró Group seems to have been guaranteed, based on the abundance of fluvial, lacustrine and floodplains facies (Cladera et al., 2002, 2007, Archangelsky, 2003; Limarino et al., 2012) together with the relative diversity of ferns and bryophytes. The palaeo community of Cerro Bayo was probably developed under a temperate to warm climate. If dry conditions were also present, they were mostly seasonal.

7. Conclusions

- The palynological assemblages of the Anfiteatro de Ticó Formation in the Cerro Bayo locality at Bajo Grande area consists of 124 taxa: 77 spore taxa, 39 pollen taxa (including

four angiosperms), fungi spores and eight algae. Freshwater algae and fungi spores are recorded for first time at this palynological assemblage

- 73 species are reported for first time at Cerro Bayo locality, including 26 that are identified for the first time in the Anfiteatro de Ticó Formation.
- Three major botanical groups not represented in the megafloora (i.e. lycophytes, hornworts and angiosperms) are recorded in the palynological assemblages.
- Dispersed mesofossil assemblages are described for the first time for the Baqueró Group, and provide one of the few reports of this kind for southern South America.
- The vegetation of the Anfiteatro de Ticó Formation in the Bajo Grande area may have been mainly represented by gymnosperms growing in a temperate to warm climate. The tree canopy was mainly composed by Podocarpaceae and Cheirolepidiaceae (if the habit of this latest was arborescent) and in lesser extent Araucariaceae. Ferns, cycads and bennettites would have developed in the understory. Several places with wetter habitats, perhaps swamps or ponds, would have allowed the development of bryophytic, lycophytic, aquatic ferns and angiosperms communities within this generally more restricted humid context.
- The integration of floristic data from mega, meso and microfloral records, including relative abundance analyzes, with sedimentological traits, allows proposing an ecological scenario for the Bajo Grande area during the late Aptian. Although the assemblages reported suggest the development of very similar plant communities, subtle differences are recognized. While those preserved in L1 and L2 seem to have developed into floodplains with water instability within a delta that flows into a lake; that of L3 probably grew into a more stable area out of the flooding influence.
- The palaeo community of Cerro Bayo was probably developed under a temperate to warm climate and, if dry conditions were also present, they were mostly seasonal.

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Figure I. 1. Map showing outcrops of Baqueró Group (gray) in the Deseado Massif Basin; 2. Detail of the Cerro Bayo (Bajo Grande area). Modified from Passalia et al. (2016).

Figure II. A stratigraphic log of the Anfiteatro de Ticó Formation and the lowermost levels of Bajo Tigre Formation (BT Fm) in the Cerro Bayo (Bajo Grande area), illustrating the three fossiliferous levels (L1: BA Pal 6390, 6386; L2: BA Pal 6287, 6388; L3: BA Pal 6389).

Figure III. Quantitative distribution of major palynomorph groups from Anfiteatro de Ticó Formation at Cerro Bayo (Bajo Grande area) in the five studied samples, expressed in percentages of total palynoflora.

Plate I. 1. *Aequitriradites plicatus* Archangelsky and Archangelsky 2006, BA Pal 6387-1:O25/3; 2. *Concavissimisporites montuosus* (Döring) Fensholt 1987, BA Pal 6390-8:G44/0; 3, 4. *Contignisporites* sp., BA Pal 6388-5:C45/0; 5. *Crybelosporites berberoides* Burger 1976, BA Pal 6390-2:J40/1; 6. *Crybelosporites stylosus* Dettmann 1963, BA Pal 6390-8:C54/0; 7. *Crybelosporites* sp., BA Pal 6390-3:G49/1; 8-9. *Distanulisporites* sp., 8. BA Pal 6389-5:P39/4; 9. BA Pal 6389-5:O44/2; 10. *Foveosporites labiosus* Singh 1971, BA Pal 6388-7:M54/4; 11. *Foveosporites* sp. cf. *F. canalis* Balme 1957, BA Pal 6388-11:T44/2; 12, 13. *Interulobites sinuosus* Scott 1976; L. BA Pal 6390-8:F34/4; BA Pal 6388-5:Y49/1; 14. *Klukisporites foveolatus* Pocock 1964, BA Pal 6388-3:D33/0; 15, 16. *Klukisporites* sp., BA Pal 6386-3:V57/0; 17. *Leptolepidites verrucatus* Couper 1953; BA Pal 6389-5:P49/0; 18.

Leptolepidites proxigranulatus Brenner 1963, BA Pal 6387-9:P55/0; 19. *Lycopodiacidites ambifoveolatus* Brenner 1963, BA Pal 6390-8:R45/1; 20. *Matonisporites cooksoni* Dettmann 1963, BA Pal 6390-6:H34/1; 21, 22. *Peromonolites* sp.; 21. BA Pal 6389-5:O22/1; 22. BA Pal 6389-20-2:F29/0; 23. *Perotrilites* sp. cf. *P. linearis* (Cookson and Dettmann) Evans 1970, BA Pal 6390-7:T56/4; 24. *Perotrilites* sp., BA Pal 6387-3:S23/4; 25. *Policingulatisporites reduncus* (Bolkhovitina) Playford and Dettmann 1965, BA Pal 6390-9:X59/3. Scale bar=10 μm .

Plate II. 1–2. *Pilunsporites muratus* Archangelsky and Archangelsky 2006, BA Pal 6390-8:F28/1; 3. *Retitriletes* sp. cf. *R. facetus* (Dettmann) Srivastava 1972, BA Pal 6390-8:C49/2; 4. *Retitriletes circolumenus* (Cookson and Dettmann) Backhouse 1978, BA Pal 6388-11:A59/0; 5. *Ruffordiaspora* sp., BA Pal 6389-7:Y58/3; 6. *Alisporites grandis* (Cookson) Dettmann 1963, BA Pal 6390-7:Z57/1; 7. *Podocarpidites astrictus* Haskell 1968, BA Pal 6386-8:T42/2; 8. *Podocarpidites epistratus* Brenner 1963, BA Pal 6386-3:U57/1; 9. *Podocarpidites otagoensis* Couper 1953, BA Pal 6386-3:S54/4; 10. *Vitreisporites* sp., BA Pal 5389-5:K30/2; 11, 12. Aberrant *Clavipollis*; 11. BA Pal 6386-4:P51/0; 12. BA Pal 6386-2:T32/4; 13. *Leiosphaeridia* sp. 1, BA Pal 6386-3:N26/4; 14. *Leiosphaeridia* sp. 2, BA Pal 6386-7:Z29/1; 15, 16. Fungi spores, 15. BA Pal 5389-1:S47/1; 16. BA Pal 6386-8:W43/1; 17. Cf. *Jushinghipollis ticoensis* Llorens and Perez Loinaze 2016, BA Pal 6387-2:N57/3; 18. *Clavatipollenites* sp. 1, BA Pal 6386-8:D51/2; 19, 20. *Clavatipollenites* sp. 2, BA Pal 6387-7:S31/2. Scale bar=10 μm .

Plate III. 1–2. CBY-1, note two simple papillae over stomatal aperture (ostiole), BA Pal 6389-8:U29/4; 3–5, CBY-2, White arrowhead indicate epidermal cells with lobate papillae; 3–4. BA Pal 6389-9:V43/0; 5. BA Pal 6389-9:B22/0; 6. CBY-3, white arrowheads indicate

epistomatic chamber with a ring of papillose cells, BA Pal 6389-1:O37/2; 7–8, CBY-4, BA Pal 6389-9:H38/0; 9–10, CBY-6, BA Pal 6389-8:M35/0; 11–12, CBY-5, BA Pal 6389-8:G41/0; 13–14, CBY-7, note two simple papillae over stomatal aperture (white arrowheads) and strongly cutinized papillae on epidermal cells, BA Pal 6389-8:P25/0. Scale bar=20 μm , with exception 1,3,6, K scale bar=50 μm and 8 scale bar=10 μm .

Plate IV. 1–2. CBY-8, note papillae oriented toward the stomatal aperture (ostiole); 1. BA Pal 6389-9:Y23/4; 2, BA Pal 6389-3:Y25/1; 3–4, CBY-10, BA Pal 6389-9:R29/4; 5, CBY-9, note papillae strongly developed, BA Pal 6389-9:W51/2; 6, *Brachyoxylon baqueroensis* Martínez 1968, BA Pal 6389-8:Y25/3; 7–8, CBY-11, black arrowheads indicate polar subsidiary cells elongated; 7, BA Pal 6389-8:Q23/0, 8, BA Pal 6389-8:Q39/4; 9–11, *Brachyoxylon baqueroensis* Vera and Césari 2013: 9. Oblique section showing features of the longitudinal radial and tangential sections. White arrows indicate uniseriate rays in longitudinal tangential section, and black arrow indicates uniseriate araucarioid pitting in the radial walls of the tracheids; 10, 11 cross fields showing multiple cupressoid pits. Scale bar=20 μm , with exception 2 scale bar=10 μm , 9 scale bar=100 μm and 1,5,6,8 scale bar=50 μm .

Table I. Stratigraphic distribution and relative abundance of sporomorph species identified from Anfiteatro de Ticó Formation at Cerro Bayo (Bajo Grande area) (L1-3), 1, rare (up to 5 specimens); 2, common (6-10 specimens); 3, frequent (11 to 15); 4, abundant (16-25 specimens); 5, very abundant (more than 25 specimens) (*Uncertain affinity).

Palynological Level	L1	L2	L3
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Palynological Level	L1	L2	L3
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	Botanic Group	Taxon / Sample	BA Pal 6390	BA Pal 6386	BA Pal 6387	BA Pal 6388	BA Pal 6389	
SPORES	Marchantiidae	<i>Aequitriradites verrucosus</i>				1		
		<i>Aequitriradites plicatus</i> (Plate I.A)				1		
		<i>Staplinisporites caminus</i>	1	1	1	1		
		<i>Taurocusporites segmentatus</i>			1	2		
		<i>Triporoletes reticulatus</i>		1	2	1	1	
	Anthocerotidae	<i>Foraminisporites asymmetricus</i>			1	1	1	
		<i>Foraminisporites dailyi</i>		1	1	2	1	
		<i>Foraminisporites wonthaggiensis</i>		1	1		1	
		<i>Stoverisporites lunaris</i>	1	1	3	3	3	
	Lycopodiidae	Selaginellales	<i>Ceratosporites setosus</i>				1	
			<i>Ceratosporites equalis</i>	1	1	1	1	1
			<i>Foveosporites</i> sp. cf. <i>F. canalis</i> (Plate I.K)				1	
			<i>Foveosporites labiosus</i> (Plate I.J)				2	
	Lycopodiiales	<i>Densoisporites velatus</i>	1		1	1	2	
		<i>Densoisporites corrugatus</i>	1		1	1	2	
		<i>Lycopodiacidites ambifoveolatus</i> (Plate I.S)	1					
<i>Retitriteles baqueroense</i>			1	1	4	1		

	Botanical Group	Taxon / Sample	BA Pal 6390	BA Pal 6386	BA Pal 6387	BA Pal 6388	BA Pal 6389
SPORES	Incertae sedis	<i>Concavissimisporites</i> sp. cf. <i>C. penolaensis</i>				1	
		<i>Coptospora foveolata</i>				1	1
		<i>Distalanulisporites</i> sp. (Plate I.H-I)					5
		<i>Empardecisporites apiverrucata</i>	1	1	1	1	1
		<i>Interulobites sinuosus</i> (Plate I.L,M)		1	2	3	
		<i>Leptolepidites verrucatus</i> (Plate I.Q)			1		
		<i>Leptolepidites major</i>	1		1	1	1
		<i>Leptolepidites proxigranulatus</i> (Plate I.R)			1		
		<i>Nevesisporites similiscaris</i>			1	2	
		<i>Nevesisporites vallatus</i>			1		
		<i>Peromonolites</i> sp. (Plate I.U,V)					5
		<i>Perotrilites</i> sp. cf. <i>P. linearis</i> (Plate I.W)	1				
		<i>Perotrilites</i> sp. (Plate I.X)			5		
		<i>Pilunsporites muratus</i> (Plate II.A,B)	1				
		<i>Policingulatisporites reductus</i> (Plate I.Y)		1	1		1
	<i>Rugulatisporites neuquensis</i>				1		
LIV GRAM	Pteridosper	<i>Alisporites gracilis</i> (Plate		1			

Monilophyta		<i>Retitriletes circolumenus</i> (Plate II.D)	1	1		1	
		<i>Retitriletes douglasii</i>	3	1	1	1	1
		<i>Retitriletes</i> sp. cf. <i>R. facetus</i> (Plate II.C)	1				
		<i>Retitriletes austroclavatioides</i>				1	1
		<i>Appendicisporites potomacensis</i>		1		2	2
	<i>Appendicisporites unicus</i>				1	1	
	<i>Cicatricosisporites potomacensis</i>	1					
	<i>Cicatricosisporites annulatus</i>		1	1	1	2	
	<i>Cicatricosisporites cuneiformis</i>		1	1	1	1	
	<i>Cicatricosisporites hughesi</i>				1	1	
	<i>Klukisporites foveolatus</i> (Plate I.N)				1	3	
	<i>Klukisporites</i> sp. (Plate I.O,P)		5				
	<i>Plicatella baqueroensis</i>		1	1	3	3	
	<i>Ruffordiaspora ludbrookiana</i>			1			
	<i>Ruffordiaspora australiensis</i>		1	1	1		
	<i>Ruffordiaspora</i> sp. (Plate II.E)		1	1	1	1	
	<i>Trilobosporites purverulentus</i>		1	2	1		
	Gleicheniaceae	<i>Clavifera</i> sp.		1		1	
		<i>Gleicheniidites senonicus</i>	5	3	3	5	2
		<i>Gleicheniidites aptianus</i>				1	
<i>Gleicheniidites</i> sp. 3 in Llorens 2008					1		

Pinidae	mophyta	II.F)						
		<i>Vitreisporites signatus</i>	5	5	1	1	3	
		<i>Vitreisporites</i> sp. (Plate II.J)	1	1	1		1	
	Cheirolepidiaceae	<i>Classopollis triangulus</i>			1			
		<i>Classopollis classoides</i>		3	3	3		
		<i>Classopollis chateaunovi</i>	1					
		<i>Classopollis rieseri</i>		1				
	Araucariaceae	<i>Classopollis</i> spp. (Plate II.K,L)	5	5	5	5	5	
		<i>Cyclusphaera psilata</i>	5	2	2	3	3	
		<i>Cyclusphaera radiata</i>	3	1	1	1	1	
		<i>Cyclusphaera</i> sp.	5	1	1	1	1	
		<i>Araucariacites australis</i>	2			3	2	
		<i>Araucariacites spinosus</i>	1					
		<i>Balmeiopsis limbatus</i>		1	1	1		
		Podocarpaceae	<i>Callialasporites trilobatus</i>		3	2	4	3
			<i>Callialasporites dampieri</i>					1
			<i>Callialasporites turbatus</i>		2			
	<i>Callialasporites microvelatus</i>			1			1	
	<i>Callialasporites segmentatus</i>			2				
	<i>Gammeroites</i> sp. A in Arch. and Villar de Seoane 2005			1				
	<i>Gammeroites volkheimeri</i>	1	1	1	1	1		
	<i>Dacrydiumites praecupressinoides</i>		1		1			

	<i>Ornamentifera</i> cf. <i>O. tuberculata</i>				1	
Pteridaceae	<i>Contignisporites</i> (Plate I.C,D)				1	
	<i>Contignisporites burgueri</i>	1			1	1
	<i>Contignisporites cooksoniae</i>			1	3	1
Polyodiaceae	<i>Sotasporites triangularis</i>	1				
	<i>Sotasporites elegans</i>		1		1	
Dicksoniaceae or Cibotiaceae	<i>Cibotioidites auriculatus</i>				1	1
Dicksoniaceae (aff. Lophosoria)	<i>Cyatheacidites tectifera</i>	1	1	1	2	1
Osmundaceae	<i>Baculatisporites comaumensis</i>					1
	<i>Osmundacidites diazii</i>		1	1	2	2
Cyatheaceae, Dicksoniaceae or Schizaeaceae (aff. Lygodium)	<i>Cyathidites australis</i>		1	1	1	1
	<i>Cyathidites minor</i>	3	3	3	3	3
	<i>Cyathidites patagonica</i>	3	3	3	3	3
	<i>Cyathidites punctatus</i>				2	
Marsileaceae	<i>Crybelosporites berberoides</i> (Plate I.E)	1				
	<i>Crybelosporites stylosus</i>	1				

	<i>Microcachrydites antarcticus</i>		2	1	2	
	<i>Podocarpidites verrucosus</i>	1	3			1
	<i>Podocarpidites marwickii</i>	1	3	1	1	3
	<i>Podocarpidites ellipticus</i>	2	3	2	2	4
	<i>Podocarpidites auriculatus</i>		3	1	1	3
	<i>Podocarpidites astrictus</i> (Plate II.G)		3			1
	<i>Podocarpidites epistratus</i> (Plate II.H)		2			
	<i>Podocarpidites otogoensis</i> (Plate II.I)		2		1	
	<i>Podocarpidites vestitus</i>		1			1
	<i>Trichotomosulcites microsaccatus</i>	1	2	1	2	3
Ephedrales	<i>Ephedripites multicostatus</i>		1			
Incertae sedis	<i>Ticoites gamerroi</i>		1	1		4
	<i>Cycadopites follicularis*</i>		3	1	1	1
Angiosperms	cf. <i>Jusinghipollis ticoensis</i> (Plate II.Q)		1			
	<i>Clavatipollenites</i> sp. 1 (Plate II.R)			1		
	<i>Clavatipollenites</i> sp. 2 (Plate II.S-T)			1	2	1
	<i>Lethomasites</i> sp.*		1	1	1	
Zygnemata	<i>Ovoidites spriggii</i>		1		1	

	(Plate I.F)					
	<i>Crybelosporites</i> sp. (Plate I.G)	1				
Matoniaeae	<i>Matonisporites cooksoni</i> (Plate I.T)		1		1	
Incertae sedis	<i>Antulsporites</i> sp.			1	1	2
	<i>Antulsporites baculatus</i>	1			1	1
	<i>Capsispora vulcanica</i>	1				
	<i>Cibotiumspora juncta</i>					1
	<i>Concavissimisporites montuosus</i> (Plate I.B)				2	
ceae	<i>Ovoidites parvus</i>			2		1
	<i>Ovoidites reticulatus</i>			1	1	
	<i>Ovoidites</i> sp.	1				
	<i>Lecaniella foveata</i>					1
Botryococaceae	<i>Botryococcus</i> sp.			2	1	2
Prasinophyceae	<i>Leiosphaeridia</i> sp. 1 (Plate II.K)			5		
	<i>Leiosphaeridia</i> sp. 2 (Plate II.N)			5		
UNC	Dispersed spores (Plate II.O,P)	1	1		2	1

* taxon with uncertain affinity

Table II. Stratigraphic distribution of the different morphotypes of cuticle fragments and its probable affinity.

Morphotype	Probable affinity	L1	L2	L3
	? Pteridospermatophyta (seed ferns)			
CBY-9	<i>Incertae sedis</i> (Plate IV.5)			X
	Bennettitales			
CBY-5	<i>Cycadopsis involuta</i> Menéndez 1966 (Plate III.11–12)			X
CBY-3	<i>Otozamites parviauriculata</i> Menéndez (1966), in Archangelsky and Baldoni (1972b) (Plate III.6)			X
CBY-7	<i>Ptilophyllum antarcticum</i> (Halle) Seward, in Archangelsky and Baldoni (1972b) (Plate III.13–14)			X
CBY-4	<i>Ptilophyllum longipinnatum</i> Menéndez 1966 (Plate III.7–8)			X
CBY-2	<i>Zamites grandis</i> Menéndez, in Archangelsky and Baldoni (1972b) (Plate III.3–5)			X
CBY-1	<i>Incertae sedis</i> (Plate III.1–2)	X	X	X
CBY-6	<i>Incertae sedis</i> (Plate III.9–10)			X
	Pinidae (conifers)			
CBY-8	<i>Brachyphyllum baqueroense</i> Traverso (1968) (Plate IV.1–2)			X
CBY-10	<i>Incertae sedis</i> (Plate IV.3–4)	X	X	X
CBY-11	Cheirolepidiaceae (cf. <i>Tomaxellia degiustoi</i> Archangelsky) (Plate IV.7–8)	X	X	X

Table III. Summary of species identified by megascopic plant remains in the Anfiteatro de Ticó Formation at Cerro Bayo (Bajo Grande area). L1 and L3 correspond to the fossiliferous levels identified in this study. NF Araucarites + NF II correspond to fossiliferous sections previously reported in the literature (e.g., Archangelsky, 2003 and references therein; Archangelsky and Villar de Seoane, 2004; Villar de Seoane, 2005). "Levee level" corresponds to the fossiliferous levels studied by Cladera et al. (2007).

Taxon	L1	L3	NF Araucarites + NF II	"Levee level"
Fronds of uncertain affinities				
<i>Sphenopteris baqueroensis</i> Archangelsky (1967b)			X	
<i>Sphenopteris</i> cf. <i>S. nordenskjoeldii</i> Halle, in Archangelsky (1967b)			X	
<i>Sphenopteris</i> (<i>Onychiopsis</i> ?) <i>psilotoides</i> (Stokes and Webb) Ward, in Archangelsky (1967b)		X		
<i>Sphenopteris sueroi</i> Archangelsky (1967b)		X		
Marchantiidae (liverworts)				
<i>Ricciopsis grandensis</i> Cladera et al. (2007)				X
Monilophyta				
Cyatheaceae				
<i>Cyathea cyathifolia</i> (Villar de Seoane) Villar de Seoane (1999)			X	
?				
Pteridaceae				
<i>Adiantopteris tripinnata</i> Cladera et al. (2007)				X
?				
Schizaeaceae				
Schizaeaceae <i>incertae sedis</i> Cladera et al. (2007)				X

Incertae sedis				
<i>Cladophlebis antarctica</i> (Nathorst) Halle, in Archangelsky (1967a)			X	
Pteridophyta indet.		X	X	
Pteridospermophyta (seed ferns)				
<i>Pachypteris elegans</i> Archangelsky (1966)		X		X
Cycadales				
Zamiaceae				
<i>Restrepophyllum chiguoides</i> Passalia, Del Fueyo, Archangelsky (2010)				X
Incertae sedis				
<i>Almargemia incrassata</i> Archangelsky (1966)				X
<i>Mesosingeria oblonga</i> Villar de Seoane (2005)				X
<i>Mesosingeria parva</i> Villar de Seoane (1997a)				X
<i>Pseudoctenis crassa</i> Archangelsky and Baldoni (1972a)			X	
<i>Pseudoctenis dentata</i> Archangelsky and Baldoni (1972a)				X
<i>Sueria elegans</i> Villar de Seoane (1997a)				X
<i>Sueria</i> sp.		X	X	
<i>Ticoa lamellata</i> Archangelsky (1966)			X	X
<i>Androstrobus murku</i> Archangelsky and Villar de Seoane (2004)				X
<i>Androstrobus pentagonicus</i> Archangelsky and Villar de Seoane (2004)				X
<i>Androstrobus rayen</i> Archangelsky and Villar de Seoane (2004)				X
Bennettitales				
<i>Cycadolepis lanceolata</i> Menéndez, in Baldoni (1974)				X
<i>Cycadolepis oblonga</i> Menéndez, in Baldoni (1974)				X
<i>Cycadolepis</i> sp.2 Baldoni (1974)				X
<i>Dictyozamites areolatus</i> Archangelsky and Baldoni (1972)				X
<i>Dictyozamites latifolius</i> Menéndez, in Archangelsky and Baldoni (1972b)		X	X	X

<i>Otozamites parviauriculata</i> Menéndez (1966), in Archangelsky and Baldoni (1972b)				X
<i>Ptilophyllum antarcticum</i> (Halle) Seward, in Archangelsky and Baldoni (1972b)		X	X	
<i>Ptilophyllum</i> sp.		X		
<i>Zamites grandis</i> Menéndez, in Archangelsky and Baldoni (1972b)	X	X	X	
<i>Zamites</i> sp.	X			
Ephedrales				
Ephedraceae				
e				
<i>Ephedra verticillata</i> Cladera et al. (2007)				X
Pinidae				
(conifers)				
Araucariaceae				
<i>Araucarites baqueroensis</i> Archangelsky (1966)	X			X
<i>Araucarites minimus</i> Archangelsky (1966)	X	X	X	
<i>Notopuhuen brevis</i> Del Fueyo (1991)	X	X	X	
Podocarpaceae				
<i>Apterocladus lanceolatus</i> Archangelsky (1966)	X	X	X	
<i>Podocarpus dubius</i> Archangelsky (1966)	X	X	X	
Cheirolepidiaceae				
<i>Tomaxellia bifurcata</i> Archangelsky (1966)	X	X	X	
<i>Brachyoxylon baqueroensis</i> Vera and Césari (2015)	X			
Incertae sedis				
<i>Tarphyderma glabra</i> Archangelsky and Taylor (1986)				X
<i>Brachyphyllum baqueroense</i> Traverso (1968)				X
<i>Brachyphyllum</i> sp.	X	X		
male cones indet.	X	X		

Highlights

- Upper Aptian of Patagonia palynological record of 124 taxa, including 26 new.
- First record of lycophytes, hornworts and angiosperms for the floral assemblage.
- First report of a mesofossil association for the Baqueró Group.
- Paleoenvironmental scenario by integration of multiple sources of floral remains.

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