Taylor & Francis
Taylor & Francis Group

Cretaceous angiosperm pollen from the Kachaike Formation, south-western Santa Cruz Province, Argentina

V.S. Perez Loinaze, V.D. Barreda, S. Archangelsky and A. Archangelsky

Museo Argentino de Ciencias Naturales "B. Rivadavia", Av. Ángel Gallardo 470, C1405DJR Buenos Aires, Argentina, CONICET

ABSTRACT

Thirty-three angiosperm pollen species are here reported from mid-Cretaceous deposits of the Kachaike Formation, Austral Basin, southern Argentina. *Clavatipollenites* is the most abundant angiosperm genus, with six well-defined morphological groups recognised on the basis of their reticulum morphology and sculpture. Pollen of eudicots are scarce, represented by tricolpate (*Psilatricolpites* spp. and *Tricolpites* spp.), tricolporoidate and tricolporate morphotypes (*Dryadopollis* spp.). Increasing complexity in the aperture structure is seen throughout the sequence; tricolpate and tricolporoidate forms are recorded in almost all samples, while tricolporate pollen grains are restricted to the middle and upper levels of the unit. The high species richness and abundance of monocolpate-ulcerate angiosperm related to monocots or magnoliids *sensu lato* recorded in the unit is comparable to that previously recognised in other assemblages from the early and middle Albian of the southern (e.g. Australia) and northern hemispheres (e.g. Western Portuguese basin, Europe). The recorded increase in the number of angiosperm species towards the middle and upper parts of the Kachaike Formation, with the presence of monocolpate, tricolpate, tricolporoidate and tricolporate pollen, suggests an early-early middle Albian age for these parts of the unit, in agreement with the early Albian age proposed for its basal levels on the basis of dinoflagellates.

1. Introduction

The origin and early diversification of angiosperms was a major event in the history of land plants. The earliest known angiosperms appeared in a landscape dominated by Cretaceous gymnosperms and ferns. Primitive angiosperms have been the subject of intensive study in the northern hemisphere, but records of primitive angiosperms in southern South America remain scarce despite recent efforts to improve it (Vallati 2001, 2013; Barreda and Archangelsky 2006; Archangelsky et al. 2008; Medina et al. 2008; Archangelsky et al. 2009; Archangelsky and Archangelsky 2013, among others).

The Austral Basin is located in the southernmost part of South America with a sedimentary infill of Upper Jurassic to Neogene deposits (Nullo et al. 1999). Sedimentation within this basin was affected by several marine transgressions. Arbe (2002) recognised three tectono-sedimentary cycles during the Cretaceous: the Río Mayer (Berriasian–early Aptian), the Lago San Martin (early Aptian–early Turonian) and the Lago Viedma (early Turonian–Maastrichtian) cycles. The Kachaike Formation conformably overlies the Río Mayer Formation and was deposited during the high-stand period of the Lago San Martín Cycle (Arbe 2002). This unit comprises mudstones deposited in a prodelta environment, alternating with fine-to medium-grained cross-bedded sandstones of a delta front. Lithology shows a progressive shallowing trend towards the upper part of the sequence, which is capped with fluvial deposits (Riccardi 1971). Abundant plant megafossils and

spore–pollen assemblages were previously reported from the Kachaike Formation (Halle 1913; Frenguelli 1935; Piátnitzky 1938; Baldoni and Ramos 1981; Ruiz 1984; Longobucco et al. 1985; Baldoni et al. 2001; Archangelsky and Llorens 2003, 2005, 2009; Llorens and Del Fueyo 2003; Cúneo and Gandolfo 2005; Archangelsky et al. 2012). Palynological analysis reported the presence of the angiosperm families Chloranthaceae (*Asteropollis*), Chloranthaceae or other primitive angiosperms (*Clavatipollenites*), Winteraceae (*Walkeripollis*) and Arecaceae (*Arecipites, Palmidites, Proxapertites* and *Spinizonocolpites*), along with scarce tricolpate and triporoidate pollen of eudicots (Barreda and Archangelsky 2006; Archangelsky et al. 2012) and other morphotypes of uncertain botanical affinity including *Brenneripollis, Pennipollis* (possible Alismatales or Chloranthaceae), *Retimonocolpites* and *Schrankipollis*. Cúneo and Gandolfo (2005) and Passalia (2007a, 2007b) described leaf remains collected at the Arroyo Caballo Muerto and Bajo Comisión localities, respectively, that were related to primitive angiosperms as subordinate components in these fossil assemblages. These assemblages are instead dominated by conifers, particularly Cheirolepidiaceae (*Classopollis* spp., up to 70% of the total abundance), while Araucariaceae (*Cyclusphaera, Balmeiopsis* and *Araucariacites*, up to 10%) and Podocarpaceae (*Podocarpidites* and *Callialasporites,* up to 10%) are subordinate (Archangelsky et al. 2012). Pteridophytic spores are co-dominant in the middle
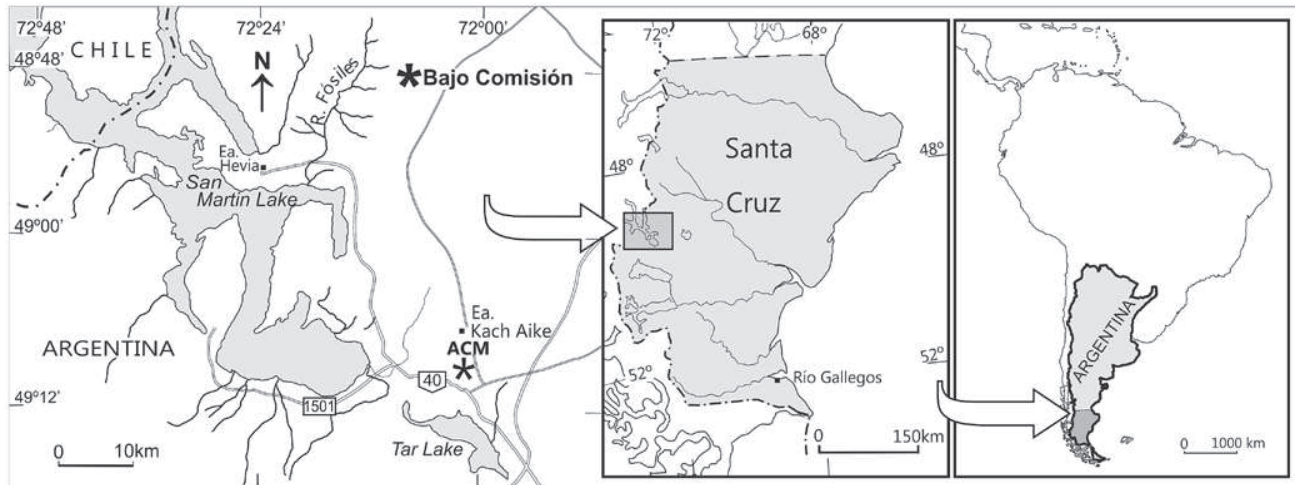
Figure 1. Location map showing the Bajo Comisión locality, modified from Barreda and Archangelsky (2006).

levels of the unit, reaching up to 50% of the total abundance (Archangelsky et al. 2012).

The Kachaike Formation is considered to be of late Aptian to early Cenomanian age on the basis of numerous paleontological studies, including ammonoids (Leanza 1970; Blasco de Nullo et al. 1980; Medina and Rinaldi 1986; Aguirre-Urreta 2002), leaf impressions (Halle 1913; Longobuco et al. 1985; Del Fueyo et al. 2008) and palynomorphs (Baldoni and Ramos 1981; Gamerro in Rebasa 1982; Baldoni et al. 2001; Guler and Archangelsky 2006; Archangelsky et al. 2012; Perez Loinaze et al. 2012).

In this study, we analysed new angiosperm pollen morphotypes recovered from the Kachaike Formation at the Bajo Comisión section of south-western Santa Cruz Province (48° 51′S, 72° 90′ W) (Figure 1). We report on changes in the angiosperm composition throughout the sequence as well as major trends in pollen morphology. These new data are evaluated in the context of the evolutionary scheme proposed for southern South America by Archangelsky et al. (2009) and compared with other palynological assemblages previously reported for middle latitudes.

2. Material and methods

Fifteen samples were processed using standard palynological techniques for extraction and concentration of palynomorphs. The organic residues were sieved using 20-μm and 10-μm mesh and mounted in glycerine jelly on microscope slides. Palynomorphs were examined with an Olympus BX-51 microscope. Photographs were taken with a Nikon DS-Fi1 digital camera. Coordinates of the illustrated specimens are given as England Finder references. The resulting slides are deposited in the Palynological Collection of the Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' (BA Pal, see Supplemental data) and stubs for SEM are deposited in the Paleobotanical Collection.
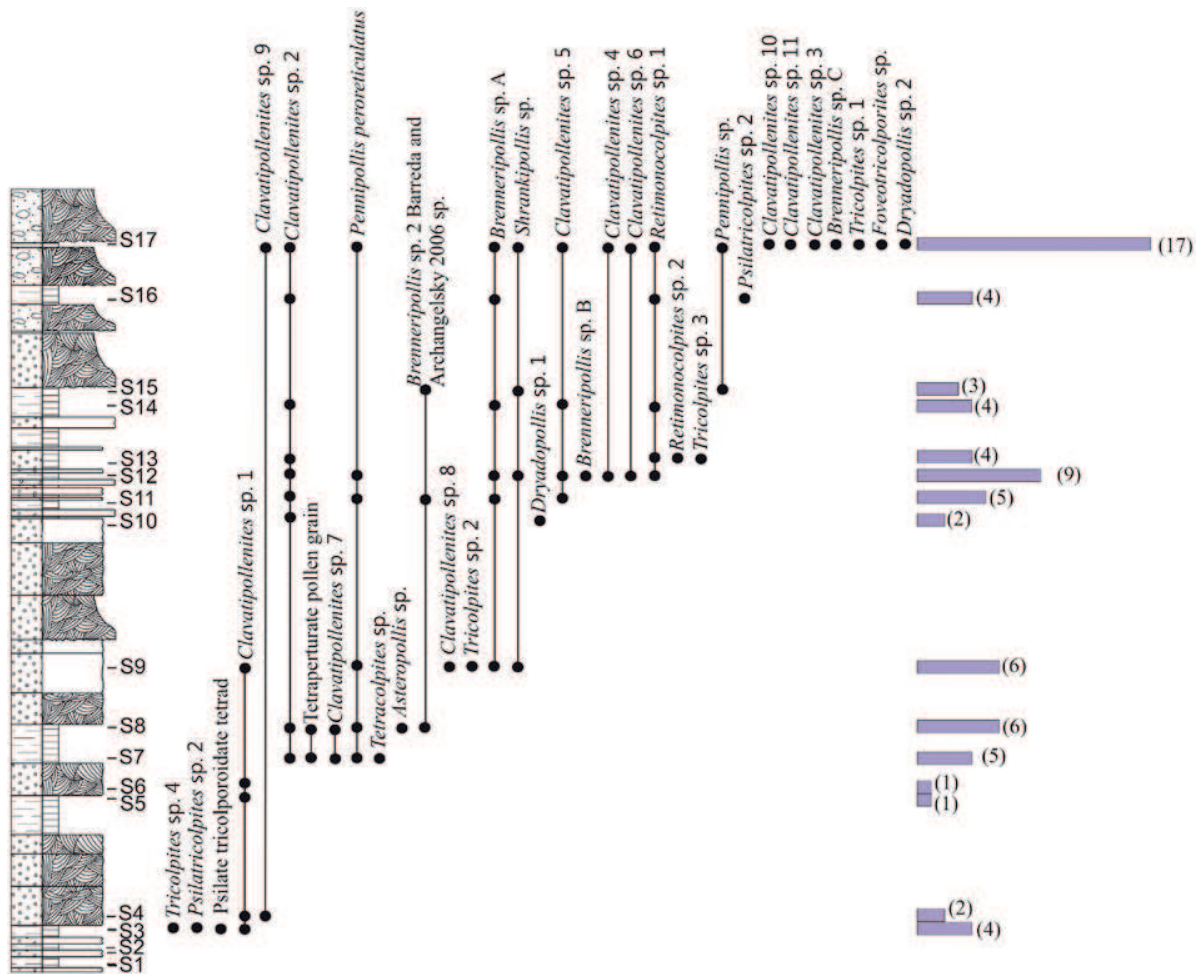
3. Results

A total of 33 angiosperm pollen morphotypes were recovered from the Kachaike Formation, with 31 of these reported for the first time. They can be attributed to Chloranthaceae and plesiomorphic Chloranthaceae-like pollen grains (12), basal eudicots (11) and *incertae sedis* angiosperms (10). These groups are briefly analysed in the following paragraphs and detailed morphological features are listed in Supplemental data; their distributions are given in Figure 2 and they are illustrated in Figures 3–5. It is noteworthy that a significant increase in the number of angiosperm morphotypes was seen through the sequence, from 1 to 4 morphotypes in the lower levels, 9 morphotypes in the middle ones and 17 morphotypes in the uppermost levels of the Kachaike Formation (Figure 2).

3.1. Chloranthaceae and plesiomorphic Chloranthaceae-like pollen grains

The genus *Clavatipollenites* is used here in a broad sense to encompass semitectate, monocolpate-ulcerate to trichoto-mocolpate pollen grains, similar to pollen of the extant Chloranthaceae or other related lineages (Couper 1958; Doyle et al. 1975; Walker and Walker 1984; Friis et al. 2011). However, most of the features of *Clavatipollenites* have been interpreted as plesiomorphic (Doyle and Endress 2014; Doyle 2015) and as a result, this taxon may represent basal angiosperm lineages not necessarily closely related with Chloranthaceae. *Clavatipollenites* is the most abundant and diverse angiosperm genus recovered in the Kachaike Formation. These pollen grains are globose, with variable apertures ranging from ulcerate, monocolpate, trichotomocolpate to almost 'triaperturate' (with the apertures located in a subequatorial position). This is a highly variable character in *Clavatipollenites* and, even within a single morphotype, different types of apertures can be observed. This is especially true in those specimens with an irregular reticulum (Groups I and II, Figure 6). The sculpture is reticulate with muri and lumina of variable size. Some specimens show a reticulum with scattered round and large luminae that clearly contrast with the normal microreticulate pattern usually seen in *Clavatipollenites*. For the moment, we consider these structures to be preservation artefacts (secondary structure). However, some of us (SA and AA) analysing synchronous Cretaceous units from Patagonia (Cerro Bayo Section at Lago Cardiel) observed similar structures in well-preserved specimens that can be definitively attributed to the original morphology.
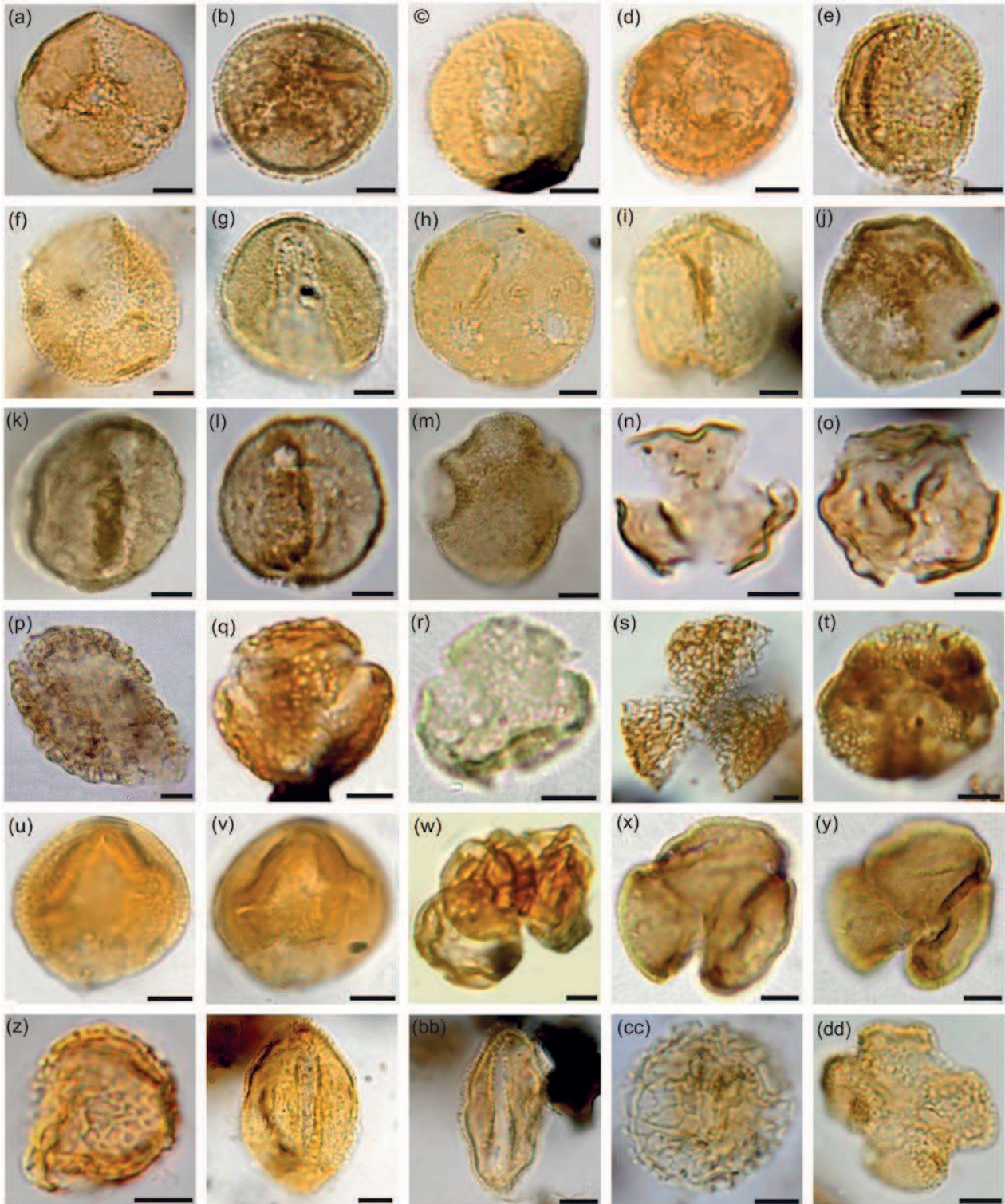
Figure 2. Stratigraphic distribution of the angiosperm pollen species recovered from the Kachaike Formation, Bajo Comisión locality. Numbers on the right represent the angiosperm species number recorded for each sample.

The ornamentation on the muri, when present, is composed of small grana. In contrast to the variable nature of the aperture, this sculptural feature remains constant within each species. This allowed us to recognise six well-defined morphological groups that show a particular distribution through the unit (Figure 6).

Group I (represented by *Clavatipollenites* sp. 1, Figures 3 (a)–(d) and 4(a)–(c)) is present from the basal to middle levels of the Kachaike Formation (Figure 6) and is characterised by a poorly defined reticulum with smooth muri (variable in width), and thin and high columellae. Several specimens of this group show a broken reticulum with a partially detached sexine. The aperture of *Clavatipollenites* sp. 1 is highly variable, ranging from triulcerate-porate (Figure 4(a)), trichotomocolpate (Figures 3(b) and (d) and 4(b) and (c)) to monocolpate (Figure 3(c)). Forms with a trichotomocolpate aperture are referred by some authors to other genera, such as *Jusinghipollis* Jansonius and Hill (1987) (=*Singhipollis* Juhász and Góczán 1985). We prefer to retain our trichotomocolpate morphotype, together with the ulcerate and colpate ones within a single taxonomic unit (*Clavatipollenites* sp. 1), rather than segregating them into several less inclusive taxa with unclear taxonomic delimitation. The 'triaperturate' condition may have been derived from a trichotocolpate one with the development of a 'partially

columellate island' in the polar region. Paden Phillips and Felix (1971) proposed the species *Porotrichotomosulcus clavatus* for pollen with three or four pores forming a triradiate or quadriradiate aperture, similar to the one recorded in some specimens assigned here to *Clavatipollenites* sp 1. However, the Patagonian specimens differ from *Porotrichotomosulcus clavatus* in displaying greater variability in aperture configuration. Ward (1986) considered *Porotrichotomosulcus clavatus* to be a variation of *Asteropollis asteroides*, an approach followed by Burger (1980) and Wintage (1980). Considering both the closest botanical affinity of *Asteropollis*is to extant *Hedyosmum* and that *Hedyosmum* pollen grains have four to six (usually five) apertures (Walker and Walker 1984; Eklund et al. 2004; Doyle and Endress 2014), we prefer to retain these specimens within *Clavatipollenites* sp. 1.
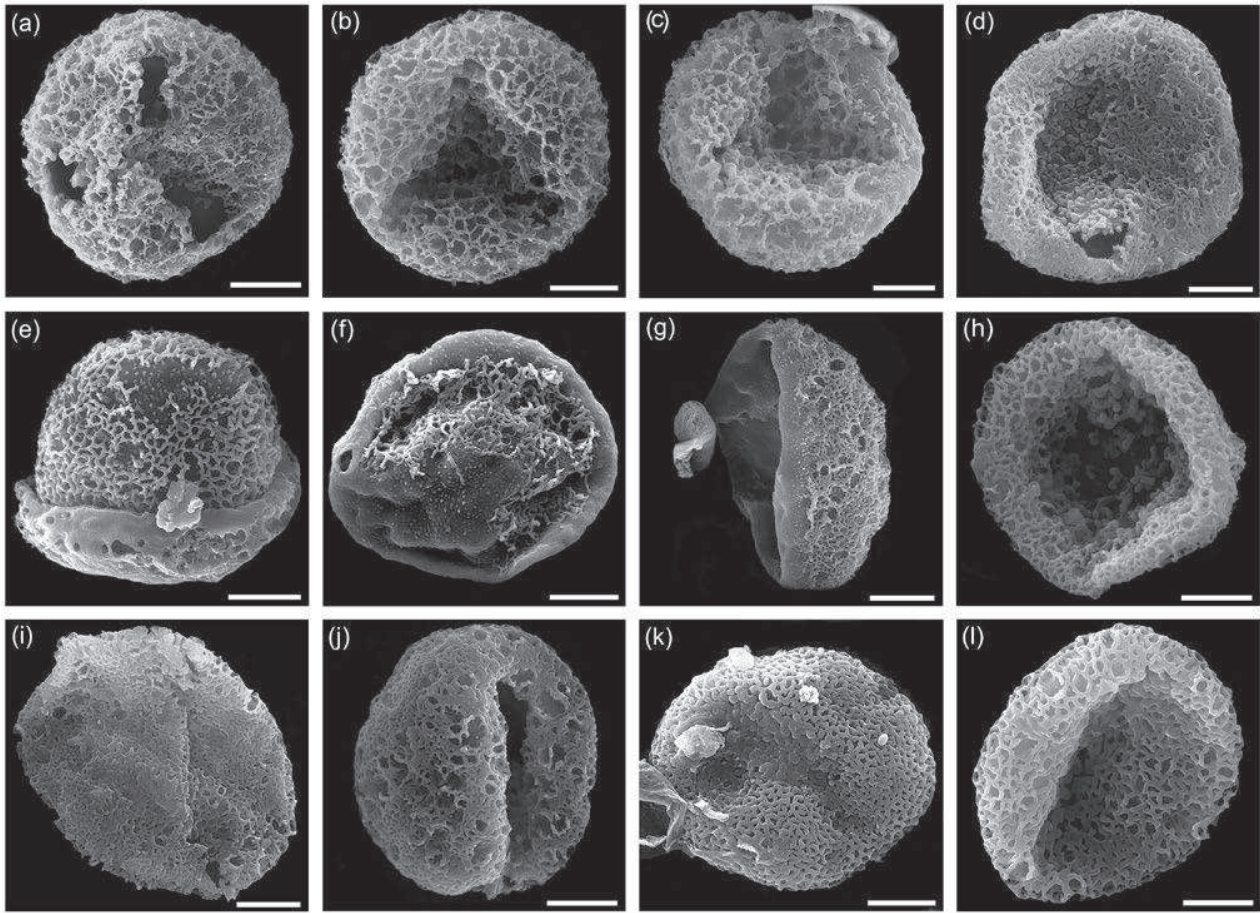
Group II (represented by *Clavatipollenites* sp. 2 (Figures 3(f)–(h) and 4(d)) and *C.* sp. 3 (Figure 4(e)–(g)) is present from the middle to upper levels of the Kachaike Formation (Figure 6) and characterised by a well-defined and irregular reticulum (muri of variable width and lumina of variable morphology). These species differ both in their muri width and aperture type (Supplemental data). *Clavatipollenites* sp. 2, in particular, has poorly defined apertures: colpate (Figures 3(g) and

Figure 3. (a)–(d) *Clavatipollenites* sp. 1; (a) BA Pal 5862-2: Y30/1; (b) BA Pal 5862-1: G41/0; (c) BA Pal 61074: V41/0; (d). BA Pal 5862-2: S40/1; (e) *Clavatipollenites* sp. 4, BA Pal 5872-1: V28/0; (f)–(h) *Clavatipollenites* sp. 2; (f) BA Pal 6118: S50/0; (g) BA Pal 5872-1: J38/3; (h) BA Pal 5871-2: K27/1; (i) *Clavatipollenites* sp. 5, BA Pal 6107: P55/3; (j) *Clavatipollenites* sp. 7, BA Pal 5867-1: H45/2; (k)–(l) *Clavatipollenites* sp. 6; (k) BA Pal 5871-1:N25/4; (l) BA Pal 5872-1: N55/0; (m) Tetra-aperturate pollen grain, BA Pal 5867-1: G51/2; (n) *Psilatricolpites* sp. 1, BA Pal 5875-1: U31/4; (o) *Psilatricolpites* sp. 2, BA Pal 5862-1: H36/1; (p) *Tricolpites* sp. 1, BA Pal 5876-1: Y33/4; (q) *Tricolpites* sp. 2, BA Pal 5868-1: N26/3; (r) *Tricolpites* sp. 3, BA Pal 5872-1: E41/2; (s) *Tricolpites* sp. 4, BA Pal 5862-1: R33/1; (t) *Dryadopollis* sp. 1, BA Pal 5869-1: R331/1; (u)–(v) *Foveotricolporites* sp., BA Pal 5876-2: M40/3; (w) Psilate tricolporoidate pollen, BA Pal 5862-1: S35/0; (x)–(y) *Dryadopollis* sp. 2, BA Pal 5872-1: F48/4; (z) *Brenneripollis* sp. A, BA Pal 5876-2: L35/1; (aa) *Retimonocolpites* sp. 1, BA Pal 5876-2: T46/2; (bb) *Retimonocolpites* sp. 2, BA Pal 5872-2: V51/2; (cc) *Pennipollis* sp., BA Pal 5876-2: X51/3; and (dd) *Tetracolpites* sp., BA Pal 6119: V46/3. Scale bar: 5 μm.

4(d)), trichotomocolpate (Figure 3(f)) to 'triaperturate', with apertures in a subequatorial position and a central area of free-standing columellae (Figure 3(h)). In this character, it resembles *Clavatipollenites* sp. 1, but it differs in having a well-defined reticulum.

Figure 4. (a)–(c) *Clavatipollenites* sp. 1; (d) *Clavatipollenites* sp. 2; (e)–(g) *Clavatipollenites* sp. 3; (h) and (l) *Clavatipollenites* sp. 4; (i) *Clavatipollenites* sp. 5; (j) *Clavatipollenites* sp. 6; and (k) *Clavatipollenites* sp. 7. Scale bar: 5 μm.

Groups III–VI include forms with well-defined and regular reticulum (muri with uniform width and lumina with well-defined morphology), grouping iso and heterobrochate forms. Group III (represented by *Clavatipollenites* sp. 4 (Figures 3(e) and 4(h) and (l)) *C.* sp. 5 (Figures 3(i) and 4(i)), *C.* sp. 6 (Figures 3(k) and (l) and 4(j)) and *C.* sp. 7 (Figures 3(j) and 4(k)) is present in the upper levels of the Kachaike Formation (Figure 6) and is characterised by a well-defined regular reticulum with sculptured muri of the same width as, or thinner, than the lumina. *Clavatipollenites* sp. 5 and *C.* sp. 6 are subcircular and monocolpate with a well-defined long and straight colpus. In *Clavatipollenites* sp. 6, the colpus is bordered by infoldings of the exine. The latter feature was previously recognised in *Retimonocolpites dividuus* Pierce 1961 (=*Clavatipollenites rotundus* Kemp 1968), but that species differs from *Clavatipollenites* sp. 6 in having a coarser reticulum (lumina 1–2 μm in diameter). *Clavatipollenites* sp. 7 has a trichotomocolpate aperture (Supplemental data).

Group IV (represented by *Clavatipollenites* sp. 8 (Figure 5(a)), is present from the middle to the upper levels of the unit (Figure 6) and characterised by having a well-defined regular reticulum and smooth muri of the same width as, or thinner, than the lumina.

Group V (represented by *Clavatipollenites* sp. 9 (Figure 5(b)), is present from the basal to the upper levels of the Kachaike

Formation (Figure 6) and characterised by a well-defined regular reticulum with sculptured muri, where the muri are thicker than the lumina, creating a microreticulate to tectate-foveolate appearance.
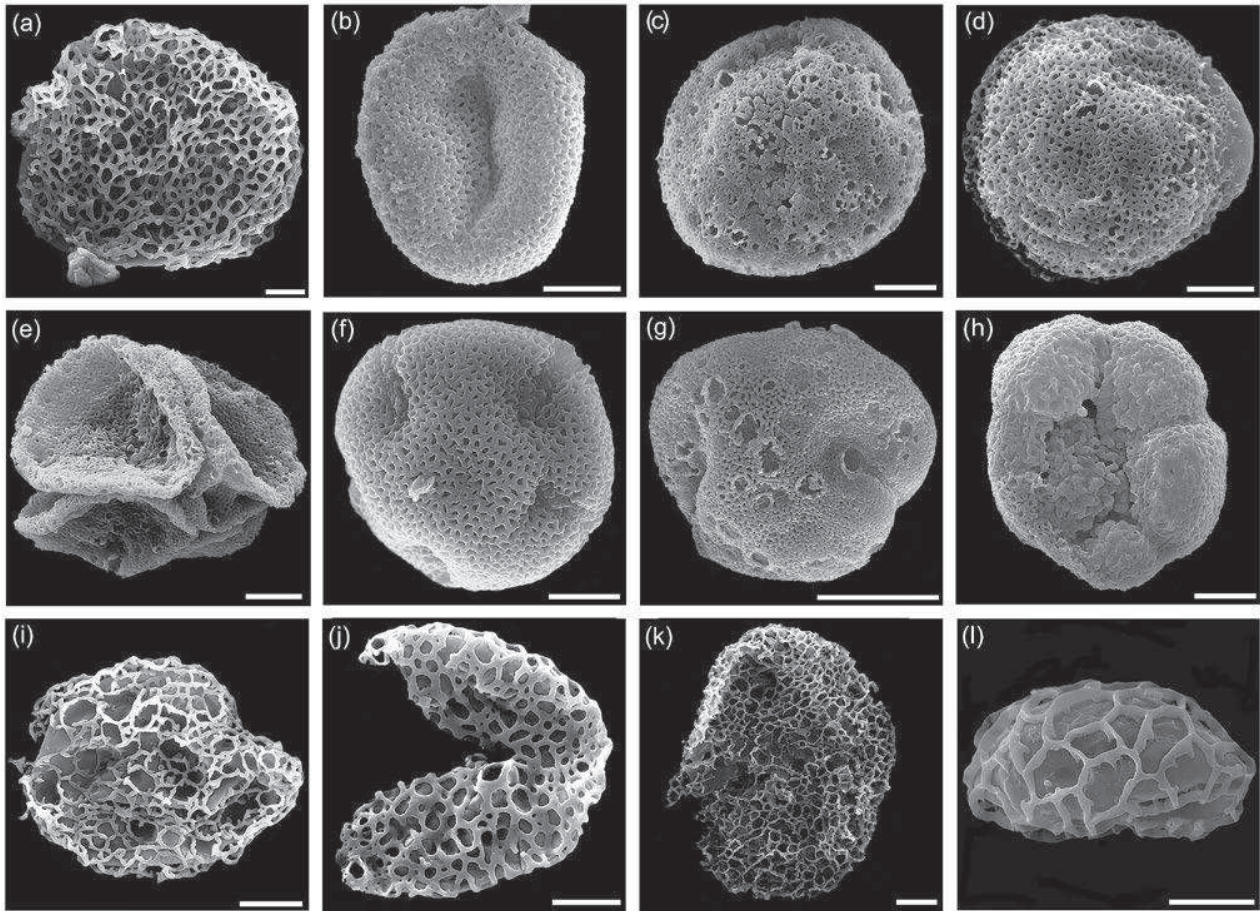
Finally, Group VI (represented by *Clavatipollenites* sp. 10 (Figure 5(c) and (d)) and *C.* sp. 11 (Figure 5(e)) is present only in the uppermost levels of the unit (Figure 6) and is characterised by a well-defined regular reticulum with smooth muri, thicker than the lumina. *Clavatipollenites* sp. 10 and *C.* sp. 11 differ in the shape and in the size of the lumina (Supplemental data).

Other chloranthaceous pollen is represented by a few specimens of *Asteropollis* sp. (Figure 5(h)), which was recorded in the middle levels of the Kachaike Formation (Figure 6). It is similar to the extant genus *Hedyosmum*.

3.2. Eudicots

A total of 11 pollen types of presumed eudicotyledonous affinities were recognised throughout the unit. This group is represented by a scarce number of specimens, but is relatively rich in terms of species diversity.

Psilate-tricolpate pollen grains, represented by *Psilatricolpites* sp. 1 (Figure 3(n)) and *P.* sp. 2 (Figure 3(o)), were recovered from the basal to the uppermost levels of the Kachaike Formation (Figure 2).

Figure 5. (a) *Clavatipollenites* sp. 8; (b) *Clavatipollenites* sp. 9; (c)–(d) *Clavatipollenites* sp. 10; (e) *Clavatipollenites* sp. 11; (f) tetraperturate pollen grain; (g) *Dryadopollis* sp. 2; (h) *Asteropollis* sp.; (i) *Brenneripollis* sp. A; (g) *Brenneripollis* sp. B; (k) *Schrankipollis* sp.; and (l) *Brenneripollis* sp. C. Scale bar: 5 μm.

Reticulate tricolpate pollen grains, represented by four species of *Tricolpites*, were recovered from the middle to the upper levels. They differ in general size, type of the reticulum and size of the lumina (Figures 2 and 3(p)–(s), Supplemental data).

Tetracolpate pollen grains assigned to *Tetracolpites* sp. (Figure 3(dd)) were also recorded in the middle levels (Figure 2), along with scarce tetra-aperturate pollen grains (Figures 3(m) and 5(f)). A tetrahedral tetrad of psilate-tricolporoidate pollen grains was recorded in the basal levels of the Kachaike Formation (Figures 3(w) and Figure 2).

Reticulate and microfoveolate tricolporate pollen grains possessing lumina that become smaller towards the apocolpi are represented by *Dryadopollis* sp. 1 (Figure 3(t)) and *D.* sp. 2 (Figures 3(x) and (y) and 5(g)) and derived from the middle levels (Figure 6). *Dryadopollis* sp. 1 is distinguishable from *D.* sp. 2 in having smaller colpi and a microreticulate exine.

The first record of a microfoveolate tricolporate form with thickened apertures was identified in the uppermost levels of the unit (Figure 2) and is represented by *Foveotricolporites* sp. (Figure 3(u) and (v)).

3.3. Other angiosperm pollen grains

Other species also recorded in the Kachaike Formation are *Pennipollis peroreticulatus*, *Pennipollis* sp. (Figure 3(cc)), *Walkeripollis* sp., *Schrankipollis* sp. (Figure 5(k)), five species

of *Brenneripollis* (two of them previously reported in Barreda and Archangelsky [2006]) and two species of *Retimonocolpites* (Figure 3(aa) and (bb)). These species do not have well-defined botanical affinities with the exception of *Walkeripollis*, which has been related to Winteraceae and *Pennipollis peroreticulatus*, which is probably related to Alismatales (Friis et al. 2000) or Chloranthaceae (Hesse and Zetter 2007; Doyle et al. 2008; Doyle 2009; Doyle and Endress 2014).

4. Discussion

This study suggests that the angiosperm richness during the mid-Cretaceous in southern South America was higher than previously thought. However, angiosperm taxa were not abundant but, in fact, subordinate within a gymnosperm-fern-dominated flora (Archangelsky et al. 2012); these results are analogous to those obtained in other mid-Cretaceous sites around the world (Crane 1987; Crane and Lidgard 1989; Crane et al. 1995; Heimhofer et al. 2007, among others). Smith et al. (2010) proposed that diversification preceded ecological abundance by an order of millions of years. Interestingly, Feild et al. (2004) suggested that the first angiosperms were trees or shrubs that established in disturbed habitats under low-light regimes. Bond and Scott (2010) suggested that the spread of angiosperms during the Cretaceous was promoted by fire regimes. As angiosperms have several key evolutionary innovations that provide them with competitive
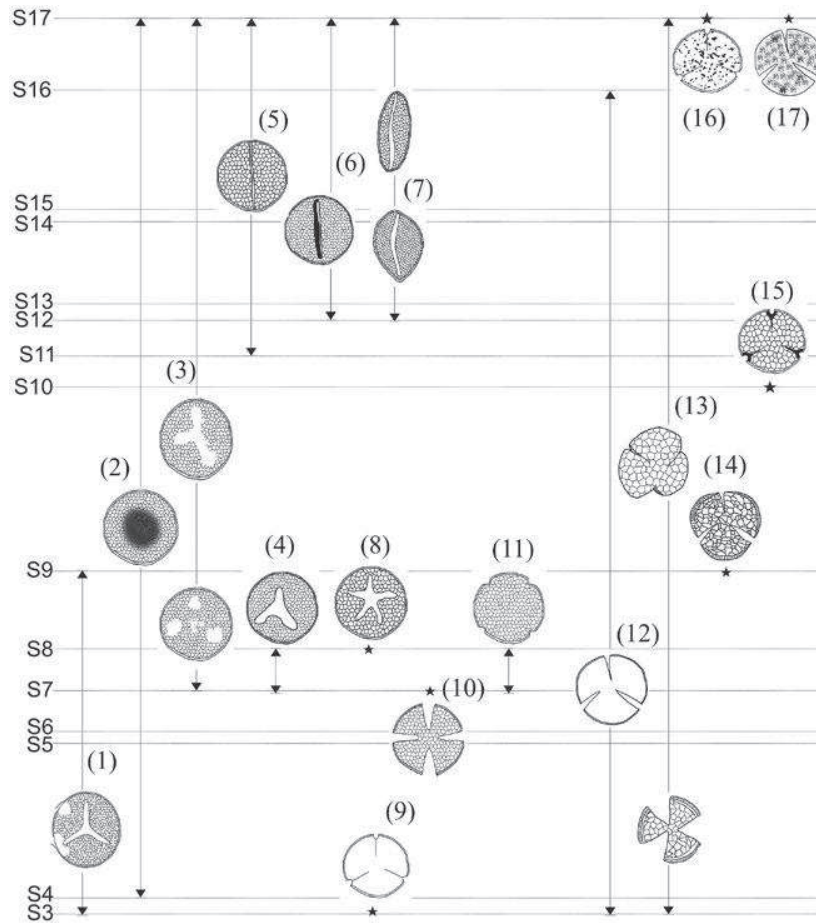
Figure 6. Stratigraphic distribution of the six morphological groups of *Clavatipollenites* recognised in the Kachaike Formation, Bajo Comisión locality. Group I, details of the specimen illustrated in Figure 4(b); Group II, details of the specimen illustrated in Figure 4(d); Group III, details of the specimen illustrated in Figure 4(l); Group IV, details of the specimen illustrated in Figure 5(a); Group V, details of the specimen illustrated in Figure 5(b); and Group VI, details of the specimen illustrated in Figure 5(d).

advantages over ferns and gymnosperms (i.e. rapid reproduction and growth, efficient hydraulic systems and life history flexibility), they could spread more efficiently because of frequent disturbances. The presence of charcoal remains in the Kachaike Formation (Passalia 2007a; Archangelsky et al. 2012) supports this assumption. Additionally, the upper levels of the unit (where the highest number of angiosperm morphospecies was recorded) also contain a great amount of charcoalified remains (Archangelsky et al. 2012).

Among angiosperms, Chloranthaceae and plesiomorphic Chloranthaceae-like pollen grains are the most abundant and richest plant groups in the Kachaike Formation. The same is true for older deposits from Patagonia (Archangelsky and Archangelsky 2013). Interestingly, the aperture configuration, feature particularly informative when identifying genera within Chloranthaceae because although there are variations these are constant within the genus (Although with variations within the family, it is constant within each genus, Martínez et al. 2013), appears to be of scarce diagnostic value within species of *Clavatipollenites*. Most Patagonian pollen grains have a highly variable aperture configuration even within the same morphospecies (ulcerate-monocolpate, trichotomocolpate to almost 'triaperturate' – *Clavatipollenites* sp. 1 and *C.* sp. 2, see Supplemental data), except in those morphotypes with a regular reticulum (e.g. *Clavatipollenites* sp. 3). Extant *Ascarina*, the closest living relative of most *Clavatipollenites* species, does display trichotomocolpate variation, although it is predominantly monocolpate (Eklund et al. 2004). In contrast, the reticulate sculpture appears to be very helpful in splitting *Clavatipollenites* specimens into different morphospecies. Hughes (1994) analysed fossil pollen from the middle Hauterivian-early Aptian of Southern England and recognised six

phases in the evolution of early angiosperms. He observed a progressively greater supratectal diversity of the semitectate-reticulate pollen towards younger deposits. Moreover, Archangelsky and Archangelsky (2013) recognised different angiosperm pollen types from the late Aptian of southern Argentina, all being semitectate-reticulate and strongly sculptured. In an analysis of living Chloranthaceae, Eklund et al. (2004) remarked that all species of *Ascarina* and *Hedyosmum* have distinct supratectal ornamentation on the muri of the reticulum, but this is lacking in *Sarcandra* and *Chloranthus*. On the other hand, *Chloranthus* exhibits polycolpoidate to polyporate pollen and *Sarcandra* is polyforate with scattered pores. The pollen found adhering onto the stigma of the floral fossils *Canrightia* and *Zlatkocarpus,* which are a stem relatives of Chloranthaceae (Doyle and Endress 2014), also lack supratectal sculpture. In the Patagonian specimens, the supratectal sculpture does not show remarkable changes through the sequence. Morphotypes with sculptured or smooth muri are represented in similar proportions all through the unit. The first ones (with supratectal sculpture on the muri) could be related to the extant *Ascarina* or *Hedyosmum*; the others (without supratectal sculture on the muri) do not possess a clear botanical affinity and may represent an extinct lineage of the Chloranthaceae or relatives or, alternatively, they may not be related to this family at all. Phylogenetic results of Doyle and Endress (2014) implied that the supratectal sculpture evolved between the divergence of *Canrightia* and *Zlatkocarpus* and the crown group of Chloranthaceae, and was later lost in the *Sarcandra* and *Chlorantus* clade.

Some general morphological trends could be recognised throughout the unit within *Clavatipollenites* species. Pollen grains with variable apertures, poorly developed reticulum (with

Figure 7. Stratigraphic distribution of the main morphological types recognised in the angiosperm pollen assemblage. (1) Subcircular pollen with irregular poorly defined reticulum and variable aperture (*Clavatipollenites* Group I: *C.* sp. 1); (2) Subcircular pollen with poorly defined aperture (*Clavatipollenites* Groups III: *C.* sp. 4; V: *C.* sp. 9; VI: *C.* sp. 10); (3) Subcircular pollen with irregular well-defined reticulum and variable aperture (*Clavatipollenites* Group II: *C.* sp. 2); (4) Subcircular pollen with trichotomocolpate aperture (*Clavatipollenites* Group IV: *C.* sp. 7); (5) Subcircular pollen monocolpate (*Clavatipollenites* Group III: *C.* sp. 5); (6) Subcircular pollen monocolpate with thickened margin colpus (*Clavatipollenites* Group III: *C.* sp. 6); (7) Elongate monocolpate pollen (*Reticulatisporites* sp. 1 and *R.* sp. 2); (8) *Asteropollis* sp.; (9) Psilate tricolporoidate pollen (Psilate tricolporoidate grains); (10) Tetracolpate reticulate (*Tetracolpites* sp.); (11) Reticulate tetra-aperturate pollen; (12) Psilate tricolpate pollen (*Psilatricolpites* sp. 1 and *P.* sp. 2); (13) Tricolpate reticulate pollen (*Tricolpites* sp. 1, *T.* sp. 3, *T.* sp 4); (14) Tricolpate reticulate pollen with the sexine thicker in the mesocolpium (*Tricolpites* sp. 2); (15) Tricolporate reticulate pollen with colpi costae and lumina smaller at the apocolpia and colpus margin (*Dryadopollis* sp. 1); (16) Tricolporate tecto-perforate pollen with smaller foveolae at the apocolpia and colpi margin (*Dryadopollis* sp. 2); and (17) Tricolporate foveolate pollen with colpi costae (*Foveotricolporites* sp.) (*single record).

muri of variable width) and subcircular amb characterised the basal levels (S3–S9 in Figure 7). Towards the middle levels (S9–S11 in Figure 7), pollen grains with a regular reticulum, well-developed muri and regular apertures were more abundant; and in the uppermost levels, definite monocolpate pollen grains with well-defined margins were identified (S11–S17 in Figure 7). Moreover, the development of the tectum shows a similar trend, varying from poorly defined reticulum (*Clavatipollenites* sp. 1, Figure 2) in the basal level, semitectate (*Clavatipollenites* sp. 2–8, Figure 2) to almost tectate-foveolate (*Clavatipollenites* sp. 9, 10 and 11, Figure 2) at the top of the unit.

Other angiosperms are represented by few specimens. In particular, eudicots are rare elements of these assemblages, but show a significant species richness. Aperture structures become more complex through the sequence. Tricolpate and tricolporoidate forms are recognised from the basal levels of the Kachaike Formation (Figure 7), and tricolporate pollen appears from the middle levels (S10) onwards. The presence of three apertures represents an important evolutionary advantage in having a higher number of available sites for germination (Furness and Rudall 2004). From the middle levels upwards, pollen grains with thickened aperture margins were identified (Figure 7), and it is possible that the presence of thickenings around the colpi or pores may result in an advantage by acting as a harmomegathic mechanism (Payne 1981).

Other species were recorded throughout the unit (*Brenneripollis* and *Pennipollis*), in the middle and upper levels (*Schrankipollis*) or as only isolated records (*Walkeripollis* and *Retimonocolpites*) (Figure 2).

Archangelsky et al. (2009) proposed three stages in the evolution of early angiosperms for southern South America based on the known records of fossil leaves and pollen grains. The third stage, assigned to the middle Albian–Coniacian time interval, is characterised by a relatively diverse angiosperm assemblage with tricolporoidate and tricolporate pollen grains since the base of this zone. The spore–pollen assemblage recorded in the Kachaike Formation may be correlated with

the lower part of this 'third stage' (middle-late Albian). This is also in agreement with an early Albian age suggested for the most basal levels of the Kachaike Formation on the basis of their dinoflagellate content (Guler and Archangelsky 2006). These author recognised important biostratigraphic species such as *Dinopterygium cladoides, Muderongia tetracantha* and *Prolxosphaeridium conulum*, and referred these assemblages to the early Albian *Muderongia tetracantha* Interval Zone proposed by Helby et al. (1987).

Several mid-Cretaceous palynological assemblages of mid-latitudes are characterised by the presence of tricolpate, tricolporoidate and tricolporate pollen grains. In Argentina, in particular, the closest palynological assemblage is that from the Huincul Formation (Albian–Cenomanian *Fraxinoipollenites fragilis* Assemblage Zone, [Vallati 2001, 2006]). Both, the Kachaike and the Huincul Formation assemblages share the presence of many spore and gymnosperm species, and among angiosperms, *Retimonocolpites, Clavatipollenites* and tricolpate, tricolporoidate and tricolporate pollen grains. However, in the *Fraxinoipollenites fragilis* Assemblage Zone, angiosperms are dominant. The Bajo Barreal Formation (=Cañadón Seco Formation), San Jorge Gulf Basin, dated as Cenomanian in age (91 ± 0.49 Ma; Bridge et al. 2000), shares many angiosperm and gymnosperm pollen grains, but the number of angiosperm morphotypes in the latter is also higher. General similarities were also recorded with assemblages from the Margas Verdes Formation (late Albian/Cenomanian), Austral Basin, but pollen documentation of this unit is still very meagre for detailed comparisons.

Similar assemblages to those recovered from the Kachaike Formation have been described from early and middle Albian units of mid-latitudes of the southern and northern hemispheres, with high diversity of monocolpate pollen and the presence of tricolpate taxa (Doyle and Robbins 1977; Burger 1993; Heimhofer et al. 2007; among others).

In Australia (Eromanga and Surat Basins), the middle Albian is marked by the first appearance of tricolporoidate pollen grains (Burger 1993) that characterised the upper part of the *Coptospora paradoza* Zone. Assemblages from this Australian Zone and those of the Kachaike Formation also share the presence of several monocolpate types and the genera *Dryadopollis* and *Tricolpites*.

The high number of morphotypes and the relative high abundance of monocolpate–ulcerate angiosperm pollen, related to monocots or magnoliids recorded in the Kachaike Formation, are comparable to that of previously recognised in assemblages from the classical continental sequences of the northern hemisphere of eastern USA (Potomac Group) and western Portugal (Algarve and Lusitanian Portuguese Basins). They also share the presence of the *Dichastopollenites/Schrankipollis/Afropollis* complex, *Brenneripollis* and/or *Pennipollis* (Doyle and Robbins 1977; Doyle et al. 1982; Doyle 1992; Heimhofer et al. 2007). In particular, the ratios between triaperturate forms (eudicots) and monocolpate pollen (monocots–magnoliids) presented by Hochuli et al. (2006) for early-middle Albian assemblages from the Portuguese Basin are comparable to those obtained here from the Kachaike Formation (<0.5 in the Portuguese Basin, ranging between 0.2 and 0.4 in the Kachaike Fm.). The *E/M-M* ratio from the Kachaike Formation was also compared with the values from the classical Potomac Group presented by Hochuli et al. (2006). The upper part of the Zone I of the Potomac Group, characterised by monocolpate and the first record of tricolpate grains, has a *E/M-M* ratio of 0.3, and this values suddenly rises to 1.3 in Subzone IIA (Hochuli et al. 2006). On the base of this sudden change, Hochuli et al. (2006) suggested the presence of a hiatus beetwen these zones. These authors proposed an early Albian age from the upper part of Zone I and a middle-late Albian age for the Subzone IIA/B. Doyle and Upchurch (2014) agree with an age of the Zone I reaching the early Albian, but suggested that the hiatus is shorter, restricting the Subzone IIA of the middle Albian.

Based on this new pollen evidence, the middle and upper parts of the Kachaike Formation can be tentatively assigned to the early-early middle Albian, in agreement with an early Albian age assignment proposed for the basal levels of this unit on the basis of dinoflagellates.

References

Aguirre-Urreta MB. 2002. Invertebrados del Cretácico Inferior [Lower Cretaceous invertebrates]. In: Haller MJ, editor. XV Congreso Geológico Argentino Geología y Recursos Naturales de Santa Cruz; Calafate. p. 439–459.

Arbe HA. 2002. Análisis estratigráfico del Cretácico de la Cuenca Austral [Stratigraphic analysis of the Cretaceous of Austral basin]. In: Haller MJ, editor. XV Congreso Geológico Argentino Geología y Recursos Naturales de Santa Cruz; Calafate. p. 103–128.

Archangelsky A, Archangelsky S, Poire DG, Canessa ND. 2008. Registros palinológicos en la Formación Piedra Clavada (Albiano) en su área tipo, provincia de Santa Cruz, Argentina [Palynological data on Piedra Clavada Formación (Albian) from its type area, Santa Cruz Province, Argentina]. Rev Mus Argent Cienc Nat ns. 10(2):185–198.

Archangelsky A, Llorens M. 2003. Palinología de la Formación Kachaike, Cretácico Inferior de la Cuenca Austral, provincia de Santa Cruz. 1. Esporas lisas y cinguladas [Palynology of the Kachaike Formation, Lower Cretaceous of the Austral basin, Santa Cruz province]. Ameghiniana. 40(1):71–80.

Archangelsky A, Llorens M. 2005. Palinología de la Formación Kachaike, Cretácico Inferior de la Cuenca Austral, provincia de Santa Cruz. 2. Esporas [Palynology of the Kachaike Formation, Lower Cretaceous of the Austral Basin, Santa Cruz province. II. Spores]. Ameghiniana. 42(2):311–328.

Archangelsky A, Llorens M. 2009. Palinología de la Formación Kachaike, Cretácico Inferior de la Cuenca Austral, provincia de Santa Cruz. Granos de polen de Gimnospermas [Palynology of the Kachaike Formation, Lower Cretaceous of the Austral Basin, Santa Cruz province. Gymnosperm pollen grains]. Ameghiniana. 46(2):225–234.

Archangelsky S, Archangelsky A. 2013. Aptian angiosperm pollen from the Ticó Flora Patagonia, Argentina. Int J Plant Sci. 174(3):559–571.

Archangelsky S, Archangelsky A, Cladera G. 2012. Palinología y paleoambientes en el perfil de Bajo Comisión (Cretácico), provincia de Santa Cruz, Argentina [Palynology and paleoenvironments of the

Bajo Comisión section, Cretaceous of Santa Cruz province, Argentina]. Rev Mus Argen Cienc Nat ns. 14(1): 23–39.

Archangelsky S, Barreda V, Passalia MG, Gandolfo M, Prámparo M, Romero E, Cúneo R, Zamuner A, Iglesias A, Llorens M, et al. 2009. Early angiosperm diversification: evidence from southern South America. Cretac Res. 30:1073–1082.

Baldoni A, Askin RA, Ragona D. 2001. Palynology of the lower cretaceous Kachaike Formation, Santa Cruz province, Argentina. In: Goodman DK, Clark RT, editors. Proceeding of the IX International Palynological Congress, 1996. Houston, TX: American Association of Stratigraphic Palynologists Foundation. p. 191–200.

Baldoni AM, Ramos V. 1981. Nuevas localidades con plantas fósiles cretácicas en la Cordillera Patagónica (provincia de Santa Cruz, República Argentina) [New locations with fossil plants Cretaceous in the Patagonian Cordillera (Santa Cruz province, Argentina Republic)]. In: Segemar, editor. VIII Congreso Geológico Argentino. Vol. 4. San Luis: Actas. p. 472–759.

Barreda V, Archangelsky S. 2006. The southernmost record of tropical pollen grains in the mid-Cretaceous of Patagonia, Argentina. Cretac Res. 27:778–787.

Blasco de Nullo G, Nullo F, Proserpio CA. 1980. Santoniano–Campaniano: estratigrafía y contenido ammonitífero [Santonian-Campanian: stratigraphy and ammonitíc content]. Cuenca Austral Rev Asoc Geol Argent. 35(4):467–499.

Bond WJ, Scott AC. 2010. Fire and the spread of flowering plants in the Cretaceous. New Phytol. 188:1137–1150.

Bridge JS, Jalfin GA, Georgieff SM. 2000. Geometry, lithofacies, and spatial distribution of Cretaceous fluvial sandstone bodies, San Jorge Basin, Argentina: outcrop analog for the hydrocarbon-bearing Chubut Group. J Sediment Res. 70(2):341–359.

Burger D. 1980. Palynology of the Lower Cretaceous of the Surat Basin. Aus Bur Miner Resour Geol Geophys Bull. 189:1–106.

Burger D. 1993. Early and middle Cretaceous angiosperm pollen grains from Australia. Rev Palaeobot Palyno. 78:183–234.

Couper RA. 1958. British Mesozoic microspores and pollen grains. Palaeontogr Abt B. 103:75–179.

Crane PR. 1987. Paleobotanical evidence on the early radiation of non-magnoliid dicotyledons. Plant Syst Evol. 162:165–191.

Crane PR, Friis EM, Pedersen KR. 1995. The origin and early diversification of angiosperms. Nature. 374:27–33.

Crane PR, Lidgard S. 1989. Angiosperm diversification and paleolatitudinal gradients in Cretaceous floristic diversity. Science. 246:675–678. http://dx.doi.org/10.1126/science.246.4930.675

Cúneo R, Gandolfo MA. 2005. Angiosperm leaves from the Kachaike Formation, Lower Cretaceous of Patagonia, Argentina. Rev Palaeobot Palynol. 136:29–47. http://dx.doi.org/10.1016/j.revpalbo.2005.04.003

Del Fueyo GM, Archangelsky S, Llorens M, Cúneo R. 2008. Coniferous ovulate cones from the Lower Cretaceous of Santa Cruz Province, Argentina. Int J Plant Sci. 169(6):799–813. http://dx.doi.org/10.1086/522646

Doyle JA. 1992. Revised palynological correlations of the lower Potomac Group (USA) and the Cocobeach sequence of Gabon (Barremian-Aptian). Cretac Res. 13:337–349.

Doyle JA. 2009. Evolutionary significance of granular exine structure in the light of phylogenetic analyses. Rev Palaeobot Palynol. 156:198–210. http://dx.doi.org/10.1016/j.revpalbo.2008.08.001

Doyle JA. 2015. Recognising angiosperm clades in the Early Cretaceous fossil record. Historical Biol. 27(3–4):414–429.

Doyle JA, Endress PK. 2014. Integrating early Cretaceous fossils into the phylogeny of living angiosperms: ANITA lines and relatives of Chloranthaceae. Int J Plant Sci. 175:555–600.

Doyle JA, Endress PK, Upchurch GR. 2008. Early Cretaceous monocots: a phylogenetic evaluation. Acta Mus Natl Pragae Ser B Hist Nat. 64(2–4):59–87.

Doyle JA, Jardiné S, Doerenkamp A. 1982. Afropollis, a new genus of early angiosperm pollen, with notes on the Cretaceous palynostratigraphy and paleoenvironments of Northern Gondwana. Bull Cent Rech Explor-Prod Elf-Aquitaine. 6:39–117.

Doyle JA, Robbins EI. 1977. Angiosperm pollen zonation of the continental Cretaceous of the Atlantic Coastal Plain and its application to deep wells in the Salisbury Embayment. Palynology. 1:43–78.

Doyle JA, Upchurch GR. 2014. Angiosperm clades in the Potomac Group: what have we learned since 1977? Bull Peabody Mus Nat Hist. 55(2):111–134.

Doyle JA, Van Campo M, Lugardon B. 1975. Observations on exine structure of Eucommiidites and Lower Cretaceous angiosperm pollen. Pollen Spores. 17:429–486.

Eklund H, Doyle JA., Herendeen PS. 2004. Morphological phylogenetic analysis of living and fossil Chloranthaceae. Int J Plant Sci. 165(1):107–151.

Feild TS, Arens NC, Doyle JA, Dawson TE, Donoghue MJ. 2004. Dark and disturbed: a new image of early angiosperm ecology. Paleobiology. 30:82–107.

Frenguelli J. 1935. Ptilophyllum hislopi (Oldham) en los 'Mayer River Beds' del Lago San Martín. Notas Mus La Plata Paleont. 1:71–83.

Friis EM, Crane PR, Pedersen KR. 2011. Early flowers and angiosperm evolution. Cambridge (UK): Cambridge University Press.

Friis EM, Pedersen KR, Crane PR. 2000. Fossil floral structures of a basal angiosperm with monocolpate, reticulate-acolumellate pollen from the Early Cretaceous of Portugal. Grana. 39(5):226–239.

Furness CA, Rudall PJ. 2004. Pollen aperture evolution – a crucial factor for eudicot success? Trends Plant Sci. 9(3):154–158.

Guler MV, Archangelsky S. 2006. Albian dinoflagellate cysts from the Kachaike Formation, Austral Basin, southwest Argentina. Rev Mus Argent Cienc Nat ns. 8(2):179–184.

Halle TG. 1913. Some Mesozoic plant-bearing deposits in Patagonia and Tierra del Fuego and their floras. K Svenska Vetensk Akad Handl. 51(1):1–58.

Heimhofer U, Hochuli PA, Burla S, Weissert H. 2007. New records of Early Cretaceous angiosperm pollen from Portuguese coastal deposits: implications for the timing of the early angiosperm radiation. Rev Palaeobot Palynol. 144:39–76.

Helby R, Morgan R, Partridge AD 1987. Palynological zonation of the Australian Mesozoic. Mem Ass Australas Palaeontols. 4:1–94.

Hesse M, Zetter R. 2007. The fossil pollen record of Araceae. Plant Syst Evol. 263:93–115.

Hochuli PA, Heimhofer U, Weissert H. 2006. Timing of early angiosperm radiation: recalibrating the classical succession. J Geol Soc London. 163:587–594.

Hughes NF. 1994. The enigma of angiosperm origins. Cambridge (UK): Cambridge University Press.

Jansonius J, Hills LV. 1987. Genera file of fossil spores – supplement. Spec Publ. Alberta: Department of Geology, University of Calgary.

Juhász M, Góczán F. 1985. Comparative study of Albian monosulcate angiosperm pollen grains. Acta Biol Szeged. 31:147–172.

Kemp EM. 1968. Probable angiosperm pollen from British Barremian to Albian strata. Palaeontology. 11:421–434.

Leanza AF. 1970. Ammonites nuevos o poco conocidos del Aptiano, Albiano y Cenomaniano de los Andes Australes con notas acerca de su posición estratigráfica [New or little known Aptian, Albian and Cenomanian ammonites of the Southern Andes with notes about their stratigraphic position]. Rev Asoc Geol Argent. 25(2):197–261.

Llorens M, Del Fueyo GM. 2003. Coníferas fértiles de la Formación Kachaike, Cretácico medio de la provincia de Santa Cruz, Argentina [Fertile conifers from Kachaike Formation, Middle Cretaceous, Santa Cruz province, Argentina]. Rev Mus Argent Cienc Nat ns. 5(2):241–244.

Longobuco MI, Azcuy CL, Aguirre-Urreta B. 1985. Plantas de la Formación Kachaike, Cretácico de la provincia de Santa Cruz [Plants from the Kachaike Formation, Cretaceous of the Santa Cruz provicne]. Ameghiniana. 21 (2–4):305–315.

Martínez C, Madriñán S, Zavada M, Jaramillo CA. 2013. Tracing the fossil pollen record of Hedyosmum (Chloranthaceae), an old lineage with recent Neotropical diversification. Grana. 52:61–180.

Medina FA, Archangelsky S, Guler V, Archangelsky A Cárdenas O. 2008. Estudio bioestratigráfico integrado del perfil La Horqueta (límite

Aptiano–Albiano), Lago Cardiel, Patagonia, Argentina [Integrated biostratigraphical study of La Horqueta section (Aptian-Albian boundary), Cardiel lake, Patagonia, Argentina]. *Rev Mus Argent Cienc Nat ns.* 10:141–155.

Medina FA, Rinaldi C. 1986. Ammonoideos del Albiano superior en la Formación Río Mayer de la estancia La Vega, provincia de Santa Cruz [Upper Albian ammonoids from the Río Mayer Formation from estancia La Vega, Santa Cruz Province]. Inst Ant Argent Contrib. 324:1–35.

Nullo FE, Panza JL, Blasco G. 1999. El Jurásico y Cretácico de la Cuenca Austral [The Jurassic and Cretaceous of the Austral Basin]. In: Caminos R, editor. Geología Argentina. Buenos Aires: Subsecretaría de Minería de la Nación. p. 528–535.

Paden Phillips P, Felix CJ. 1971. A study of Lower and Middle Cretaceous spores and pollen from the Southeastern United States. I. Spores. Pollen Spores. 13(2):280–348.

Passalia MG. 2007a. A mid-Cretaceous flora from the Kachaike Formation, Patagonia, Argentina. Cretac Res. 28:830–840.

Passalia MG. 2007b. Nuevas evidencias de la flora cretácica descripta por Halle (1913) en Lago San Martín, Santa Cruz, Argentina [New records of the Cretaceous flora described by Halle (1913) from San Martín lake, Santa Cruz, Argentina]. Ameghiniana. 44(3):565–595.

Payne WW. 1981. Structure and function in angiosperm pollen wall evolution. Rev Palaeobot Palynol. 35:39–59.

Perez Loinaze VS, Archangelsky S, Cladera G. 2012. Palynostratigraphic study of the Early Cretaceous Río Mayer and Kachaike Formations at the Quebrada El Moro section, Austral Basin, southwestern Argentina. Cretac Res. 34:161–171.

Piátnitzky A. 1938. Observaciones geológicas en el oeste de Santa Cruz (Patagonia) [Geological observations in western Santa Cruz (Patagonia)]. Bol Inf Petr YPF. 165:45–95.

Pierce RL. 1961. Lower Upper Cretaceous plant microfossils from Minnesota. Minn Geol Surv Bull. 42:1–86.

Rebasa M. 1982. Análisis estratigráfico y paleoambiental de la Formación Kachaike, aflorante en la barranca epónima, provincia de Santa Cruz [Stratigraphic and paleoenvironmental analysis of Formation Kachaike, outcropping in the eponymous gully, Santa Cruz] [tesis de licenciatura]. Buenos Aires (Argentina): Universidad de Buenos Aires. 52 p (Unpublished).

Riccardi AC. 1971. Estratigrafía en el oriente de Bahía de la Lancha, lago San Martín, Santa Cruz [Stratigraphy in east of Bahía de la Lancha, San Martin lake, Santa Cruz]. Rev Mus La Plata, Geol. 7:245–318.

Ruiz LC. 1984. Plantas fósiles cretácicas procedentes de la zona del Lago Cardiel, provincia de Santa Cruz [Cretaceous fossil plants from the Cardiel Lake, Santa Cruz]. Actas del IX Congreso Geológico Argentino; San Carlos de Bariloche, Argentina. Vol. 4. p. 444–454.

Smith SS, Beaulieu JM, Donoghue MJ. 2010. An uncorrelated relaxed-clock analysis suggests an earlier origin for flowering plants. Proc Nat Acad Sci. 107:5897–5902.

Vallati P. 2001. Middle Cretaceous microflora from the Huincul Formation ("Dinosaurian Beds") in the Neuquén Basin, Patagonia, Argentina. Palynology. 25:179–197.

Vallati P. 2006. Las primeras angiospermas en el Cretácico de La Cuenca Neuquina (Centro Oeste de Argentina): aspectos geológicos relacionados [First angiosperms in the Cretaceous of the Neuquén Basin (west-central Argentina): related geological aspects]. Rev Bras Paleont. 9:83–92.

Vallati P. 2013. A mid-Cretaceous palynoflora with *Tucanopollis crisopolensis* from D-129 Formation, San Jorge Gulf Basin, Argentina. Rev Bras Paleont. 16:237–244.

Walker JW, Walker AG. 1984. Ultrastructure of Lower Cretaceous angiosperm pollen and the origin and early evolution of flowering plants. Ann Missouri Bot Gard. 71(2):464–521.

Ward JV. 1986. Early Cretaceous angiosperm pollen from the Cheyenne and Kiowa Formations (Albian) of Kansas, USA. Palaeont Abt B. 202:1–81.

Wintage FH. 1980. Plant microfossils from the Denton Shale Member of the Bokchito Formation (Lower Cretaceous, Albian) in southern Oklahoma. Oklahoma Geol Surv Bull. 130:1–93.