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Late Aptian angiosperm pollen grains from Patagonia: Earliest steps in flowering plant evolution at middle latitudes in southern South America



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ABSTRACT

The angiosperm pollen record from the Anfiteatro de Ticó and Punta del Barco formations (Baqueró Group) is reported. The relevance of these floras is that they are accurately dated as late Aptian, and one of the oldest floras southern South America with fossil angiosperms. Twelve samples were studied, showing *Clavatipollenites* and *Retimonocolpites* as dominant types. A new species, *Jushingipollis ticoensis* sp. nov., is proposed. A doubtful angiosperm pollen grain, *Lethomasites* sp., is also identified and described. A multivariate analysis of similarities between different Early Cretaceous angiosperm pollen assemblages suggests that the Baqueró Group assemblages have great similarities with other coeval units from Argentina, Australia and United States, which were located in a similar paleolatitude.

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1. Introduction

The rise and diversification of angiosperms or "Darwin's abominable mystery", as it is often cited in the literature, is one of the most important events in the history of the terrestrial biota, not only because of the transformation of the vegetation but also because of the events of co-evolution that it also spurred (e.g., pollinators and dispersal agents) (e.g. Hu, Dilcher, Jarzen, & Taylor, 2008; Labandeira, Dilcher, Davies, & Wagner, 1994). The oldest undoubted records of flowering plants are from the Hauterivian–Barremian (e.g., Brenner, 1996; Hughes, 1994; Penny, 1986, 1991) and became dominant in almost all terrestrial ecosystems by the Late Cretaceous (e.g. Lidgard & Crane, 1988; Lupia, Lidgard, & Crane, 1999), displacing gymnosperms and ferns. Recent studies provide a further understanding of the history and evolution of the angiosperms (Doyle & Endress, 2014; Doyle, Endress, & Upchurch, 2008; Heimhofer, Hochuli, Burla, & Weissert, 2007; among others). Nevertheless, many topics concerning this important group are still matter of discussion, especially in South America, where despite the efforts made during the last decade to add new data, a complete picture of this major

evolutionary event remains elusive (Archangelsky et al., 2009). Other problem is the poor stratigraphic control in continental deposits, not only in South America but in different parts of the world from which angiosperm pollen grains are often recovered (Hochuli, Heimhofer, & Weissert, 2006). Thus, the oldest records of the different groups of angiosperms are still in discussion.

The outcrops of the Baqueró Group, located in Argentinean Patagonia (Fig. 1), contain one of the richest and most diverse Early Cretaceous floras in the Southern Hemisphere. This stratigraphic unit comprises three formations: Anfiteatro de Ticó, Bajo Tigre and Punta del Barco, in ascending stratigraphic order. The Anfiteatro de Ticó Formation is composed of conglomerates, cross-bedded sandstones, fine-grained sandstones, and thin interbedded tuffs deposited in lacustrine to deltaic environments (Cladera, Andreis, Archangelsky, & Cúneo, 2002). It is overlain by conglomerates and coarse-grained fluvial sandstones that characterize the Bajo Tigre Formation. Finally, the Punta del Barco Formation is composed of tuffaceous sandstones, tuffs, conglomerates, volcanic breccias and mudstones, deposited in a syn- and inter-eruptive fluvial environment (Cladera et al., 2002).

The Baqueró Group is a relevant unit for understanding the early diversification of angiosperms, especially in southern South America, not only because of its diverse mega- and palynofloras, but also because of its very precisely known age. CA-TIMS U–Pb ages of

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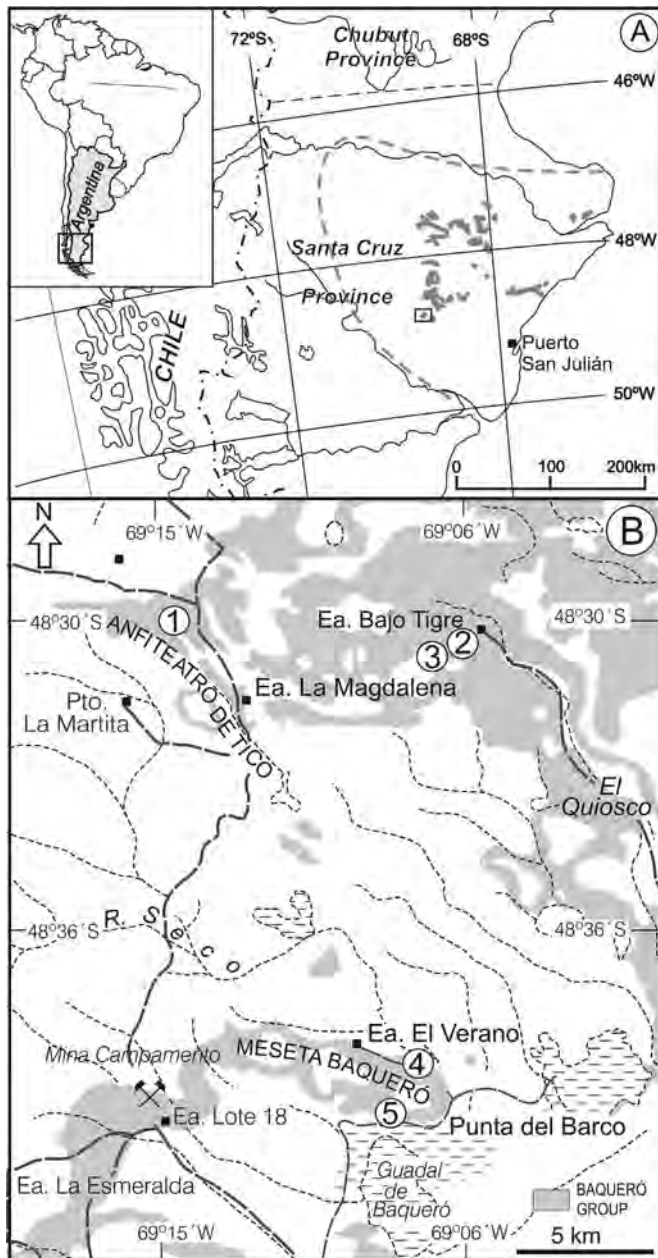


Fig. 1. (A) Location map of the studied area. (B) Details of area marked by a rectangle in A showing the Baqueró Group outcrops and the studied localities: 1, Anfiteatro de Ticó; 2, Estancia Bajo Tigre; 3, Cerro Testigo; 4, Estancia El Verano; 5, South flank of Meseta Baqueró (modified from Limarino et al., 2012).

118.23 ± 0.09 Ma from the lower levels of the Anfiteatro de Ticó Formation (Perez Loinaze et al., 2013) and 114.67 ± 0.18 Ma from the Punta del Barco Formation (Césari et al., 2011) constrain the sedimentation of the Baqueró Group to the late Aptian, and make angiosperm pollen grains from the Anfiteatro de Ticó Formation one of the oldest undoubted records of the group for southern South America.

The first reports of angiosperm remains for the Anfiteatro de Ticó Formation were made by Archangelsky and Gamero (1967), who identified dispersed pollen grains referable to *Clavatipollenites hughesii* Couper. Later, Archangelsky and Taylor (1993) studied a small anther recovered from this unit, which contained *Clavatipollenites* pollen masses. Recently, Archangelsky and Archangelsky (2013) recognized four species of *Clavatipollenites*, one of *Retimonocolpites*, and a single grain assigned to “*Anacostia*

pollen type” from the same deposits. In addition to the palynological remains, angiosperm megafloral specimens were described for the Anfiteatro de Ticó Formation by Romero and Archangelsky (1986) and Passalia, Archangelsky, Romero, and Cladera (2003). Deposits of the Bajo Tigre Formation seem to be devoid of palynomorphs, and only scattered non angiospermous megafloral remains were recovered (see a summary in Archangelsky, 2003; Limarino et al., 2012). Finally, pollen assemblages containing angiosperms from the Punta del Barco Formation were studied by Llorens (2003, 2005), whereas a leaf type with angiosperm affinities collected from the uppermost levels of this unit was described by Passalia and Cladera (2003), and later compared with the genus *Hydrocotylophyllum* (Archangelsky et al., 2009).

The main goals of this study are to provide a detailed systematic study of angiosperm dispersed pollen grains recovered from the Anfiteatro de Ticó and Punta del Barco formations, to re-examine the specimens obtained from the Punta del Barco Formation previously studied by Llorens (2003, 2005), analyze and compare the distribution and diversity of angiosperm pollen across the Baqueró Group, and finally to evaluate the results in the context of the origin and early evolution of angiosperms in South America.

2. Materials and methods

Palynological assemblages were obtained from the Anfiteatro de Ticó and Punta del Barco formations, in the center of Santa Cruz province, Patagonia, Argentina. Twelve samples were studied: 10 from the Anfiteatro de Ticó Formation (Anfiteatro de Ticó, Estancia Bajo Tigre, Cerro Testigo and Estancia El Verano localities), and two from Punta del Barco Formation (at the south flank of the Meseta Baqueró). Among the latter, one was previously studied by Llorens (2003, 2005) and is here re-examined (in Fig. 2), whereas the other (BA Pal 6236) represents a new sample. The provenance of each studied sample and its geographical coordinates are presented in Table 1 and illustrated in Figs. 1 and 2.

The palynological samples were treated following standard techniques for extraction and concentration of palynomorphs (Volkheimer & Melendi, 1976). Observations were made with an Olympus BX-51 microscope while photographs were taken with an Olympus DP25 digital camera. Coordinates of the illustrated specimens are given as England Finder coordinates. The slides are deposited in the Palynological Collection of the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (BA Pal), and the re-examined material is deposited in the Palynological Collection of the Museo Paleontológico Egidio Feruglio (MPEF PA).

To evaluate similarities among Early Cretaceous angiosperm-bearing coeval assemblages a multivariate analysis was carried out. Cluster diagrams (dendrograms) (Fig. 3) were calculated based on Bray–Curtis dissimilarity matrices, using the single linkage and the Unweighted Pair Group Method with Arithmetic mean (UPGMA) methods. The data matrix was elaborated using previously published palynological data from the Early Cretaceous of South America (e.i. Argentina, Brazil, Colombia) and from other regions with similar paleolatitudes during this period of time (i.e., Australia, Sudan, and United States). Taxonomy of early angiosperms is somewhat difficult, and many authors separate taxa using different criteria. To gain independence from taxonomic assignments and make more objective comparisons, we separated most taxa into morphological groups, based on the presence or absence of key features. For example, reticulate tricolpate pollen grains are grouped in a unique variable regardless of which taxa were originally referred. This is made to avoid problems derived from the lack of descriptions or specific assignments in some of the published records. When possible, the generic level was used as a variable (e.g. *Stellatopollis*, *Liliacidites*), without splitting it in their

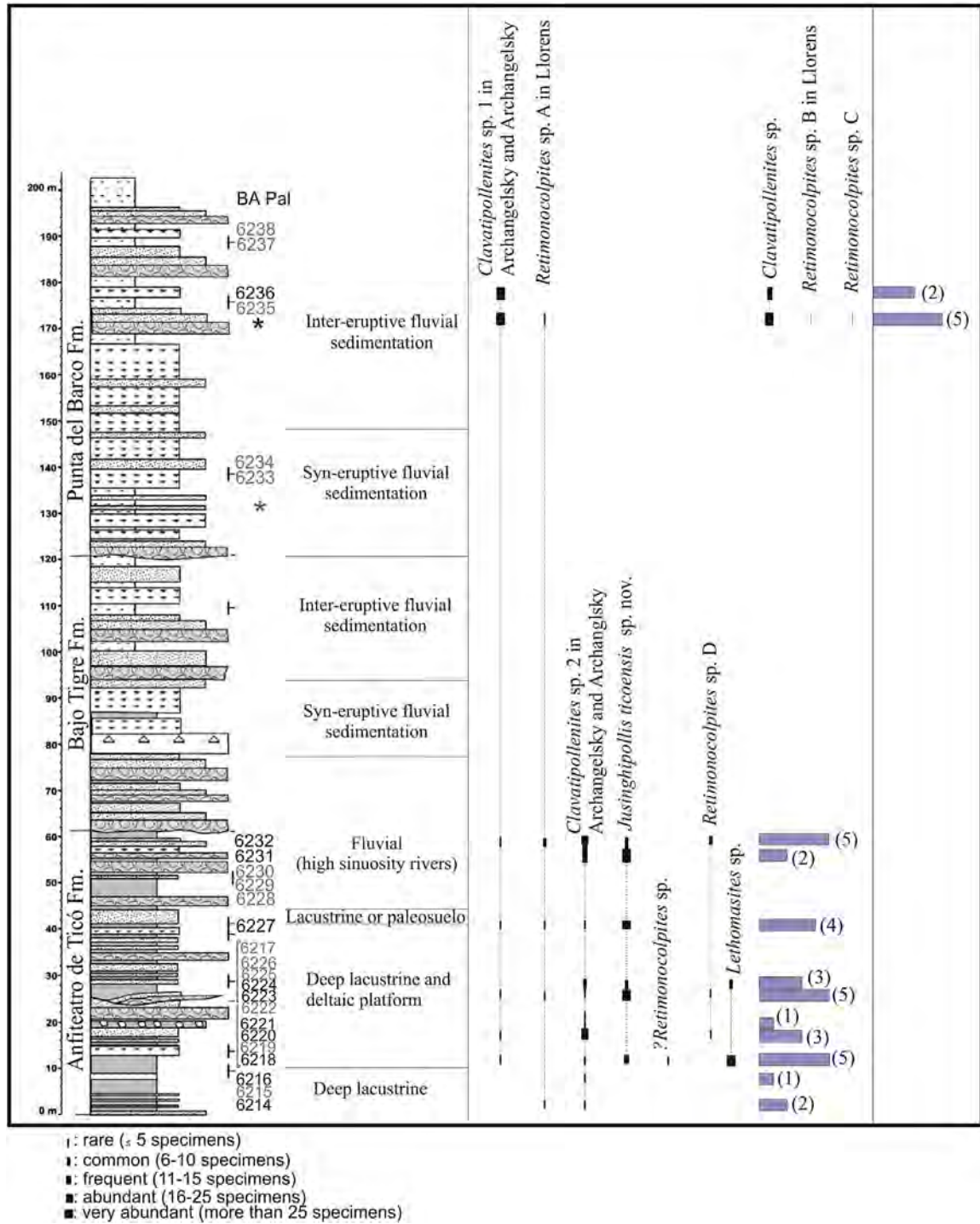


Fig. 2. Schematic stratigraphic section of the Baqueró Group showing the distribution of palynological samples, with angiosperm pollen grains (in black) and without them (in grey); * represents the re-examined sample. The number of recognized morphological types in each sample is listed at the right.

Table 1
Provenance of the studied samples.

Fm.	Locality	BA Pal	GPS coordinates
Punta del Barco	South flank of the Meseta Baquero	6236*	48°39'30"S, 69° 07'18"W
Anfiteatro de Ticó	Anfiteatro de Ticó	6218, 6223/4, 6227, 6231/2	48°30'33"S, 69°14'11"W
	Cerro Testigo	6220/1	48°30.6'0.9"S, 69°, 5.8'58"W
	Ea. El Verano	6214, 6216	48°38'29.46"S, 69°08'5.11"W

*Reexamined samples.

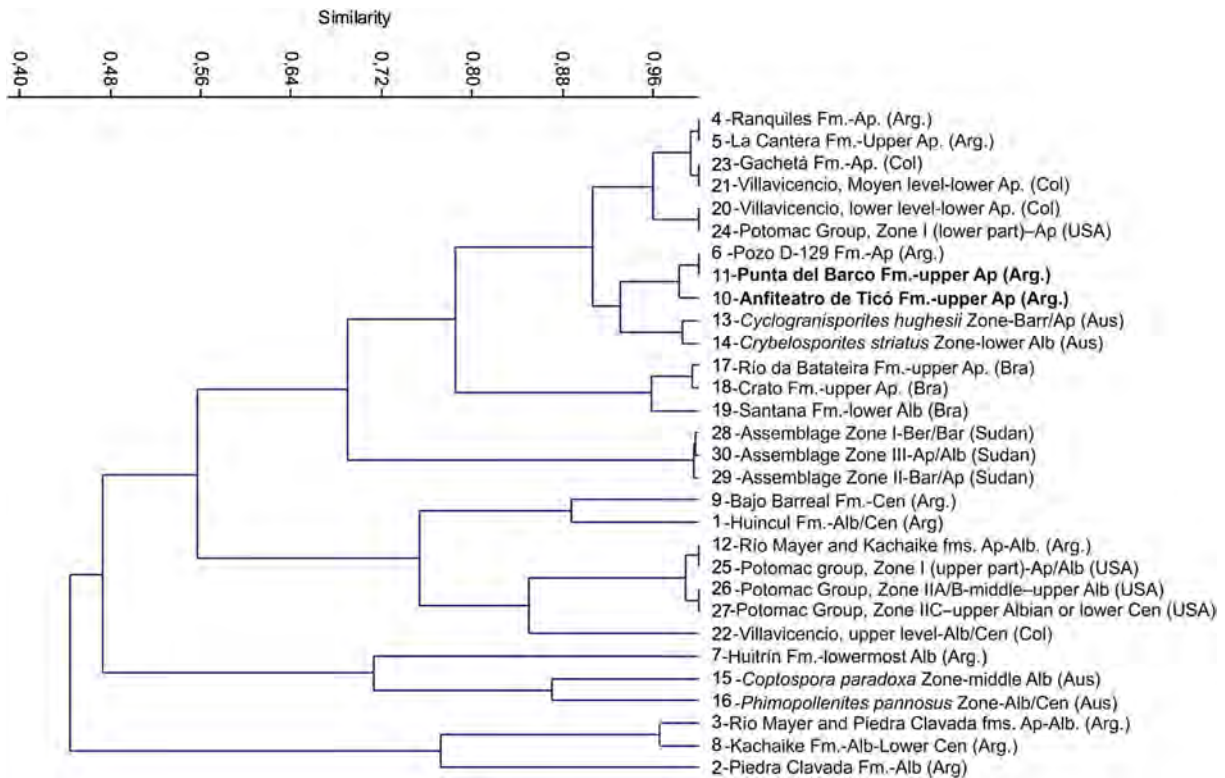


Fig. 3. Dendrogram showing the clustering of palynological assemblages from different formations and/or localities, based on Raup-Crick index, UPGMA technique (data matrix in Appendix 1) and PAST programme. Reference: Berriasian-Hauterivian: Ber/Haut; Barremian: Bar; Aptian: Ap; Albian: Alb; Cenomanian: Cen; Argentina: Arg.; Australia: Aus.; Brasil: Bra.; Colombia: Col.; 1- Huincul Fm., Neuquén Basin, Arg., Alb?– Cen (Vallati, 2001); 2- Piedra Clavada Fm. (Quebrada Don Nielsen and Tres Lagos sections), Austral Basin, Arg., Alb (Archangelsky, Archangelsky, Poiré, & Canesa, 2008); 3- Río Mayer Fm. and Piedra Clavada Fm., Austral Basin, Arg., uppermost Ap– lowermost Alb (Medina, Archangelsky, Guler, Archangelsky, & Cárdenas, 2008); 4- Ranquiles Fm. = Quili Malal Member, Rayoso Fm. (Leanza, 2003), Neuquén Basin, Arg., Ap (Vallati, 1995); 5- La Cantera Fm., San Luis Basin, Arg. (Yrigoyen, 1975), upper Ap (Prámparo, 1999); 6- Pozo D-129 Fm., San Jorge Basin, Arg., Ap (Vallati, 1996); 7- Huitrín Fm. = Quili Malal Member, Rayoso Fm. (Leanza, 2003), Neuquén Basin, Arg., lowermost Alb (Volkheimer & Salas, 1975); 8- Kachaika Fm., Bajo Comisión section, Austral Basin, Arg., Alb/lower Cen (Aguirre-Urreta, 2002; Archangelsky, Archangelsky, & Cladera, 2012; Barreda & Archangelsky, 2006; Guler & Archangelsky, 2006); 9- Bajo Barreal Fm. = Cañadón Seco Fm., Arg., Cen (91–95.8 Ma, Bridge, Jalfin, & Georgieff, 2000) (Archangelsky, Bellosi, Jalfin, & Perrot, 1994); 10- Anfiteatro de Ticó Fm., Deseado Massif Basin, Arg., upper Ap (118.23 ± 0.09 Ma, Perez Loinaze, Archangelsky, & Cladera, 2012); this work; 11- Punta del Barco Formation, Deseado Massif Basin, Arg., upper Ap (114.67 ± 0.18 Ma, Césari et al., 2011); this work; 12- Río Mayer Fm.–Kachaika Fm., Quebrada El Moro section, Austral Basin, Arg., uppermost Ap–lowermost Alb (Perez Loinaze et al., 2012); 13- Cyclogranisporites hughesii Zone, Eromanga Basin, Aus., upper Barr–Ap (Burger, 1990; Dettmann, 1973, 1994); 14- Crybelosporites striatus Zone, Eromanga Basin, Aus., lower Alb (Burger, 1990; Dettmann, 1973, 1994); 15- Coptospora paradoxa Zone, Eromanga Basin, Aus., middle Alb (Burger, 1990; Dettmann, 1973, 1994); 16- Phimopollenites pannosus Zone, Eromanga Basin, Aus., upper Alb–Cen (Burger, 1990; Dettmann, 1973, 1994); 17- Río da Batateira Fm., Araripe Basin, Bra., upper Ap (Heimhofer & Hochuli, 2010); 18- Crato Fm., Araripe Basin, Bra., upper Ap (Heimhofer & Hochuli, 2010); 19- Santana Fm., Araripe Basin, Bra., lower Alb (Heimhofer & Hochuli, 2010); 20- Villavicencio locality, Macizo del Quetame, Col., lower level, lower Ap (Pons, 1988); 21- Villavicencio locality, Macizo del Quetame, Moyen level, Col., lower Ap (Pons, 1988); 22- Villavicencio locality, Macizo del Quetame, Col., upper level, upper Alb–lower Cen (Pons, 1988); 23- Gachetá Fm., Villavicencio locality, Macizo del Quetame, Col., Aptian (Pons, 1988); 24- Potomac Group, USA, Zone I (lower part), Ap (Doyle & Robbins, 1977; Hochuli et al., 2006); 25- Potomac Group, USA, Zone I (upper part), uppermost Ap–lower Alb (Doyle & Robbins, 1977; Hochuli et al., 2006); 26- Potomac Group, Zone IIA/B, USA, middle–upper Alb (Doyle & Robbins, 1977; Hochuli et al., 2006); 27- Potomac Group, USA, Zone IIC, upper Alb or lower Cen (Doyle & Robbins, 1977; Hochuli et al., 2006; Massoni, Doyle, & Sauquet, 2015); 28- Assemblage Zone I, Sudan, Ber/Haut (Eisawi, Ibrahim, Rahim, & Schrank, 2012); 29- Assemblage Zone II, Sudan, Bar–Ap (Eisawi et al., 2012); 30- Assemblage Zone III, Sudan, Ap–Alb (Eisawi et al., 2012).

species, for the same reasons mentioned above. The data matrix of analyzed assemblages is given in Appendix A. Since morphological groups may contain several pollen species (or even genera), the total taxonomic (specific) diversity for the analyzed formation and zones is accordingly underestimated.

3. Palynological results

The studied samples preserve a rich terrestrial palynoflora, mainly composed of algae, pteridophyte spores, gymnosperm and angiosperm pollen grains (see Limarino et al., 2012). Ten of the 19 samples collected from the Anfiteatro de Ticó Formation yielded angiosperm pollen grains. For the Punta del Barco Formation, only two samples of 25 yield angiosperm pollen grains. A total of three types of *Clavatipollenites*, four of *Retimonocolpites*, and one each of *Jusinghipollenites*, and *Lethomasites* were recognized. The relative abundance and distributions of the different angiosperm pollen grains recognized along both units are given in Fig. 2 and they are illustrated in Figs. 4–7.

3.1. Systematic palynology

Genus *Clavatipollenites* Couper, 1958.

Type species. *Clavatipollenites hughesii* Couper, 1958.

Remark: *Clavatipollenites* is a genus which currently has a very broad definition (Friis, Crane, & Pedersen, 2011). In this study, we include into this genus circular to subcircular semitectate, columellate, and microreticulate pollen grains with aperture variable in shape, having irregular to well-defined margins.

Clavatipollenites sp. 1 in Archangelsky and Archangelsky (2013). (Fig. 4A–B; 6A–E).

2003 *Clavatipollenites hughesii* Couper in Llorens, pp. 235–236 (in part).

2003 *Monocolpopollenites* sp. Llorens, p. 236, Figs. 3B–C.

2005 *Clavatipollenites* sp. A Llorens, p. 92, pl. IXa–d.

Dimensions. Equatorial diameter: 12(20.6)27 μm (51 specimens).

Remarks. Some of the studied specimens have smaller diameter than the ones originally described by Archangelsky and Archangelsky (2013), but otherwise they are closely similar to the

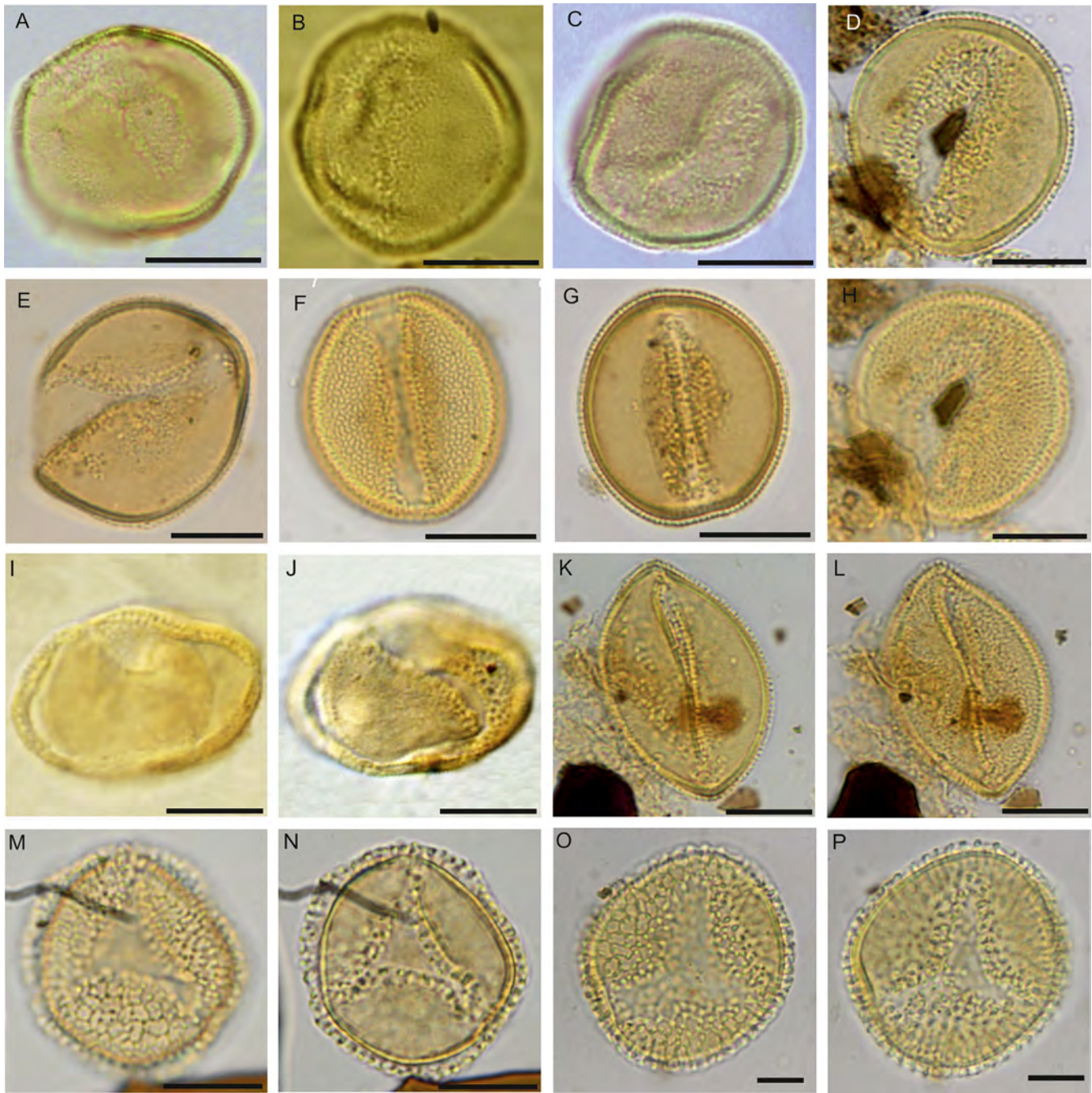


Fig. 4. A–B. *Clavatipollenites* sp. 1 in Archangelsky and Archangelsky (2013); A. MPEF PA 51b: M38/2; B. MPEF PA 51a: Q46/0; C. *Clavatipollenites* sp., MPEF PA 51a: J41/1; D, F–H. *Clavatipollenites* sp. 2 in Archangelsky and Archangelsky (2013); E. *Retimonocolpites* sp. A in Llorens, 2003, BA Pal 6223-20-1: Q31/3; F–G. BA Pal 6323-10-2: L53/4; D, H. BA Pal 6232-20-1: T28/3; I–J. *Retimonocolpites* sp. B in Llorens (2003), MPEF PA 51a: M30/0; K–L. *Retimonocolpites* sp. D, BA Pal 6232-20-1: F28/3; M–P. *Jusinghipollis ticoensis* sp. nov.; M–N. BA Pal 6223-25-1: F57/1; O–P. BA Pal 6232-20-1: W44/2, holotype. Scale bar: 10 μ m.

original description. Occasionally, *Clavatipollenites* sp. 1 in Archangelsky and Archangelsky (2013) has an almost continuous tectum across the grain or in sectors. In such cases, they are considered as tectate-perforate, but are nevertheless referred to this species because the majority of the specimens show a continuum of this character (Fig. 6C), with both types of exine organization patterns (tectate and semitectate) being present in some cases within a single specimen.

Llorens (2003) described *Clavatipollenites hughesii* Couper, 1958 for the Punta del Barco Formation based on observation of the specimens under an optical microscope. Later, based on Scanning

Electron Microscopy (SEM) results, it was possible to reassign two species: *Clavatipollenites* sp. A and *Clavatipollenites* sp. B (Llorens, 2005). Currently, it is possible to compare and assign the specimens of *Clavatipollenites* sp. A of Llorens (2005) to *Clavatipollenites* sp. 1 of Archangelsky and Archangelsky (2013), which were originally described using only SEM photographs.

Clavatipollenites sp. 2 in Archangelsky and Archangelsky (2013). (Fig. 4F–H; 6F–I).

Dimensions. Equatorial diameter: 17(23)29 μ m (76 specimens).

Remarks. *Clavatipollenites* sp. 2 in Archangelsky and Archangelsky (2013) differs from *Clavatipollenites* sp. 1 in

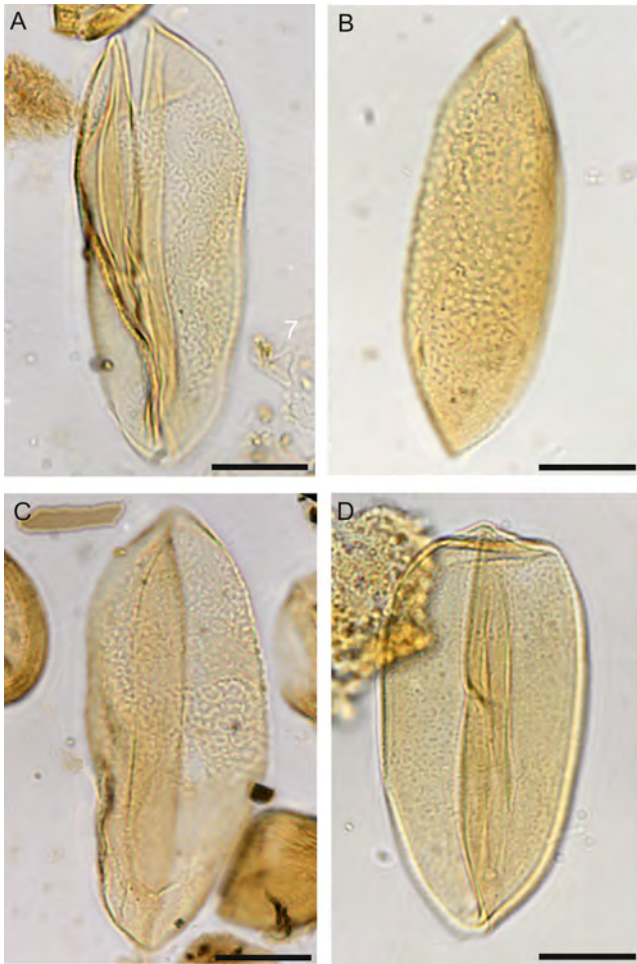


Fig. 5. A–D. *Lethomasites* sp.; A. BA Pal 6218–10–1: X49/1; B. BA Pal 6223–10–2: W51/1; C. BA Pal 6218–10–1: T52/1; D. BA Pal 6224–10–2: Q40/1; E–J. Scale bar: 10 μ m.

Archangelsky and Archangelsky (2013) by having muri that are as wide as or narrower than the diameter of the lumina.

Clavatipollenites sp.

(Fig. 4D; 6J–L).

2003 *Clavatipollenites hughesii* Couper in Llorens, pp. 235–236 (in part), Fig. 3A

2003 *Retiacolpites* sp. in Llorens, p. 238, Fig. 3G.

2005 *Clavatipollenites* sp. B in Llorens, pp. 92–93, Fig. IXe–g.

2012 *Clavatipollenites* sp. 2 in Limarino et al., Fig. 6(27)

Description. Monocolpate pollen grain, semitectate columellate, circular to subcircular amb, often folded. Colpus irregular in form and length, occasionally enclosed in a fold, and not visible. Exine microreticulate (0.9–1.2 μ m thick), thin nexine (0.2–0.3 μ m thick), sexine 0.6–0.9 μ m thick. Lumina subpolygonal to irregular in shape, 0.25–1.53 μ m in major axis. Smooth muri 0.16–0.3 μ m wide, mainly narrower than, or as wide as diameter of lumina (index muri/lumina 0.25–0.55).

Dimensions. Equatorial diameter: 24(28)30 μ m, columella width 0.15–0.2 μ m, columella length 0.6–0.8 μ m, columella separation 0.3–0.5 μ m (48 specimens).

Remarks. It is very difficult to separate *Clavatipollenites* sp. 1 in Archangelsky and Archangelsky (2013) from *Clavatipollenites* sp. under microscopic observation; however they are clearly distinguishable using SEM, due to the presence of sculpture over the tectum in C. sp. 1, and the coarser reticulum with lumina that are more irregular in shape and size in *Clavatipollenites* sp. Under light

microscopy, *Clavatipollenites* sp. possesses a mostly circular amb, and *Clavatipollenites* sp. 1 in Archangelsky and Archangelsky (2013) has a higher muri/lumina index (0.6–1.2). In addition, columellae can be easily differentiated in *Clavatipollenites* sp., because they are separated by a distance greater than their width. By contrast, in *Clavatipollenites* sp. 1 in Archangelsky and Archangelsky (2013), the width of columellae is equal to or slightly smaller than the distance between them.

Genus *Retimonocolpites* Pierce emend. Juhász & Góczán, 1985.

Type species. *Retimonocolpites dividius* Pierce, 1961.

Remark: In this study we restricted *Retimonocolpites* to include elongated to subcircular semitectate, columellate and microreticulate pollen grains with well defined monocolpate aperture.

Retimonocolpites sp. A in Llorens (2003).

(Fig. 4E; 7D–E).

2003 *Retimonocolpites* sp. A in Llorens, p. 236, Fig. 2D.

2005 *Retimonocolpites* sp. A in Llorens, p. 86–87, fig. Xc.

2012 *Retimonocolpites* sp. A in Limarino et al., Fig. 6 (30).

Description. Monocolpate pollen grain, semitectate columellate, amb oval-fusiform and frequently with sharp ends. Colpus elongate, extending along the whole length of grain. Exine microreticulate (0.8–1 μ m thick), homobrochate to slightly heterobrochate, sexine 0.3–0.35 μ m thick, nexine 0.5–0.68 μ m thick. Small lumina (0.12–0.46 μ m mayor axis), irregular to subpolygonal in shape. Muri with slightly sinuous margins (0.1–0.18 μ m wide), narrow or as wide as lumina (index muri/lumina 0.26–0.67).

Dimensions. Equatorial diameter 16–27 μ m (15 specimens).

Remarks. The sexine often appears at least partially detached. In some cases, scattered granules are found on the nexine, probably representing bases of columellae.

Retimonocolpites sp. B in Llorens (2003).

(Fig. 4I–J).

2003 *Retimonocolpites* sp. B in Llorens, p. 237, Fig. 3 E–F.

2012 *Retimonocolpites* sp. 1 Llorens, Limarino et al., Fig. 6 (29).

Dimensions. Equatorial diameter 22 μ m, polar diameter 15 μ m (1 specimen).

Retimonocolpites sp. C.

(Fig. 7A).

2012. *Retimonocolpites* sp. B, Limarino et al., Fig. 6 (28).

Description. Monocolpate pollen grain, semitectate columellate, subcircular amb. Colpus straight, length almost two-thirds of the equatorial diameter, with thickened margins (0.29 μ m wide and 0.4 μ m high), thickening smooth or with aligned small granules (0.2 μ m basal width). Microreticulate homobrochate exine. Small isodiametric lumina, subpolygonal to rounded in shape (0.25–0.5 μ m in diameter), thin muri (0.14–0.28 μ m wide), narrower than or as wide as lumina.

Dimensions. Equatorial diameter: 19 μ m (1 specimen).

Retimonocolpites sp. D.

(Fig. 4K–L; 7C).

Description. Monosulcate pollen grain, semitectate columellate, amb elliptical with acuminate apices. Colpus elongate, extending along the whole length of grain. Exine microreticulate (1–1.5 μ m thick), homobrochate, nexine smooth (0.5–0.7 μ m thick), sexine (0.5–0.8 μ m thick). Lumina irregular in shape, 0.35–0.85 μ m in maximum diameter; muri 0.15–0.35 μ m wide, narrower than or as wide as lumina (index muri/lumina 0.35–0.87). Club-shaped columellae, 0.15–0.23 μ m in basal width and 0.6–0.8 μ m in height (including capita), 0.1–0.18 μ m apart. Supramural sculpture is composed by minute coni/granules (0.1–0.14 μ m wide and 0.05–0.07 μ m tall), densely distributed.

Dimensions. Length 25–29 μ m, breadth 19–24 μ m (8 specimens).

Comparison. *Retimonocolpites* sp. A is characterized by its smaller lumina and thinner sexine, often partially detached.

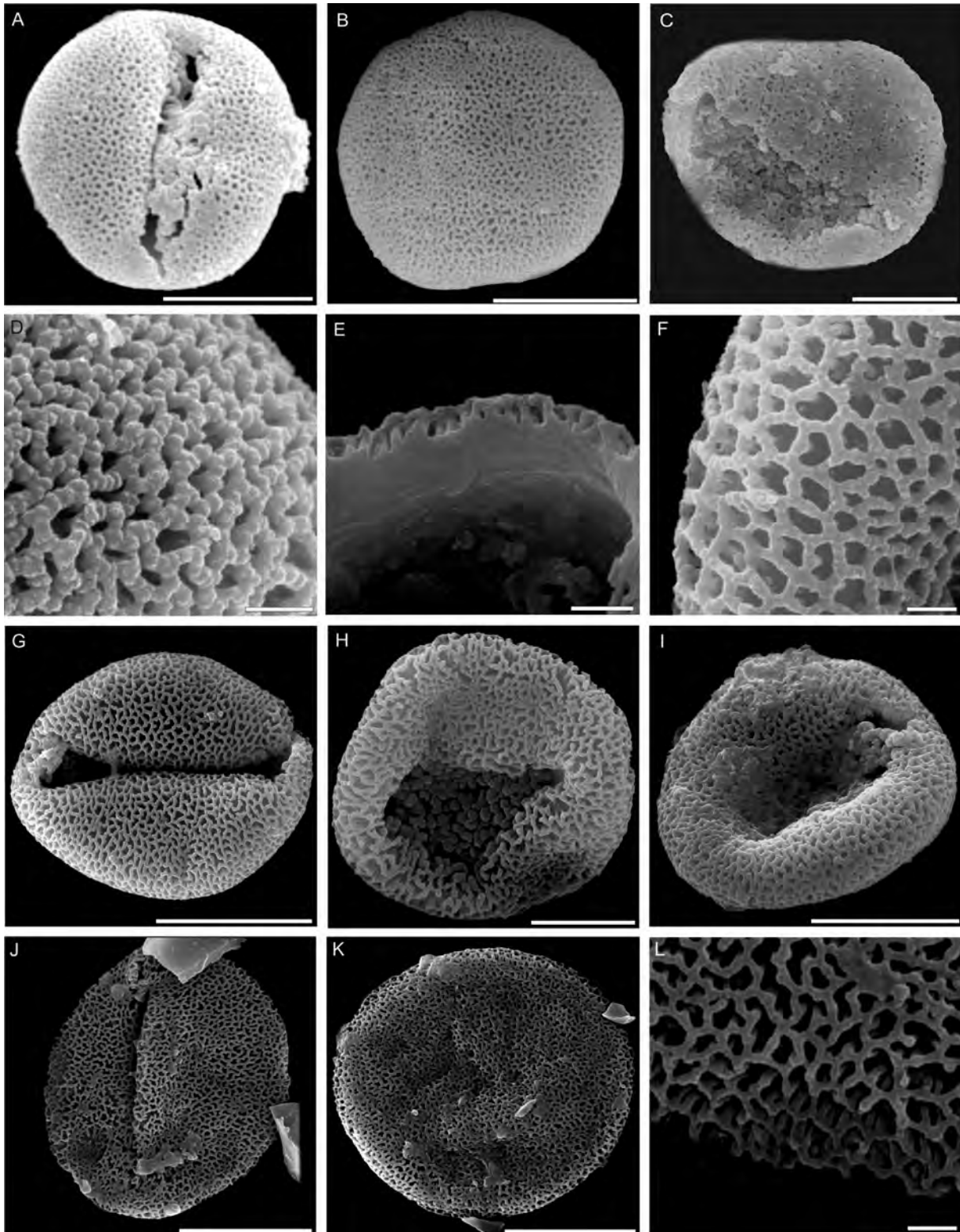


Fig. 6. A–E. *Clavatipollenites* sp. 1 in Archangelsky and Archangelsky (2013), SEM; D. Detail of supramural sculpture, SEM; E. Transverse section showing club-shaped columellae laterally fused, SEM; F–I. *Clavatipollenites* sp. 2 in Archangelsky and Archangelsky (2013), SEM; F. Detail of supramural sculpture, SEM; J–L. *Clavatipollenites* sp., SEM; L. Detail of muri, SEM. Scale bars: 10 μm (1–3, 7–11) and 1 μm (4–6, 12).

?*Retimonocolpites* sp.
(Fig. 7B).

Remarks. The single identified specimen closely compares with those described as *Retimonocolpites* sp. in Archangelsky and

Archangelsky (2013), identified in the same unit as the studied specimen. Given that we were not able to observe the aperture and the small lumina close to it. As a consequence this form is not confidently identified, and thus is left with open nomenclature,

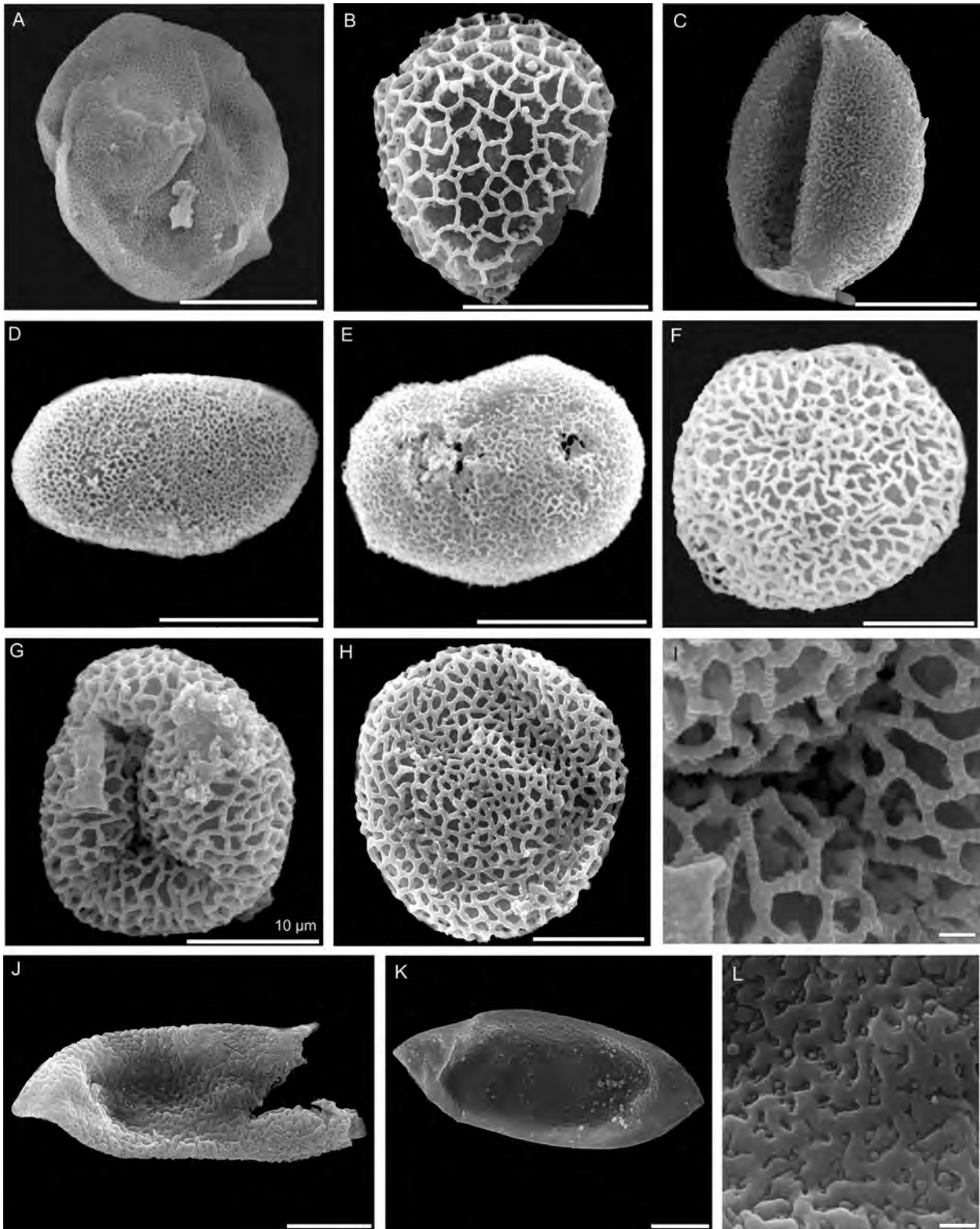


Fig. 7. A. *Retimonocolpites* sp. C, SEM; B. *Retimonocolpites* sp., SEM; C. *Retimonocolpites* sp. D, SEM; D–E. *Retimonocolpites* sp. A in Llorens (2003), SEM; F–I. *Jusinghipollis ticoensis* sp. nov, SEM; I. Detail of supramural sculpture, SEM; J–L. *Lethomasites* sp., SEM; L. Detail of exine sculpture, SEM. Scale bars: 10 µm (A–H, J–K) and 1 µm (I, L).

being referred with doubts to the genus *Retimonocolpites*.

Genus *Jusinghipollis* Jansonius & Hills, 1987.

Type species. *Jusinghipollis microreticulata* (Juhász and Góczán) Jansonius & Hills, 1987.

Remarks. Trichotomosulcate pollen grains are often assigned to *Clavatipollenites*, *Asteropollis* or different genera with trichotomosulcate

apertures, by different authors (e.g. Burger, 1993; Dettmann, 1973; Friis, Crane, & Pedersen, 1997; Heimhofer et al., 2007; Singh, 1983). *Clavatipollenites* usually is related to *Ascarina* or to *Chloranthaceae* undifferentiated, but this genus is a relatively plesiomorphic and systematically heterogeneous fossil genus (Doyle, 2015). *Clavatipollenites* type pollen grains were found associated with early

Cenomanian fruits called *Couperites*, originally related with *Chloranthaceae*, but actually this fruit may or may not be related to this family (Doyle & Endress, 2014). Certainly, *Clavatipollenites* and pollen grains of modern *Chloranthaceae* are similar, and probably many *Clavatipollenites* are true representatives of this family. However, in addition to *Chloranthaceae*, this genus probably also represents other lineages of primitive angiosperms (Doyle & Endress, 2014). On the other hand, *Asteropollis* is related to *Hedyosmum* (*Chloranthaceae*) (Doyle & Endress, 2014; Eklund, Doyle, & Herendeen, 2004; Friis et al., 2011; Walker & Walker, 1984). Hedlund and Norris (1968) originally described *Asteropollis* as tetra- or pentachotomosulcate pollen grains. Later, Walker and Walker (1984) pointed out that *Asteropollis* is basically a pentachotomosulcate grain, based on percentages obtained by Davies and Norris (1976) from *Asteropollis asteroides*: tetrachotomosulcate (30%), pentachotomosulcate (50%) and hexachotomosulcate (20%). Recently, Doyle and Endress (2014) noted that records of pre-Albian *Asteropollis* are questionable, because they present trichotomosulcate openings. Trichotomosulcate pollen may be related to *Ascarina*, which occasionally presents this aperture type (Eklund et al., 2004; Friis et al., 2011), or to *Asteropollis* and *Hedyosmum*. As it was suggested by Doyle and Endress (2014) tetra to hexachotomosulcate forms are restricted today to *Hedyosmum*, whereas the trichotomosulcate aperture is more widespread among angiosperms, and as a result these pollen grains are here considered of uncertain affinity.

Several genera have been proposed for trichotomosulcate pollen grains, such as *Oroszlanyipollis* Góczán & Juhász, 1984, *Similipollis* Góczán & Juhász, 1984 and *Singhipollis* Juhász & Góczán, 1985. *Similipollis* is a reticulate grain characterized by having smaller lumina around the aperture and at the proximal pole. *Singhipollis* was proposed to include tectate-reticulate trichotomosulcate pollen with microreticulum of uniform size all over the body. A new generic name, *Jusinghipollis*, was proposed by Jansonius and Hills (1987) to replace *Singhipollis*, because the latter was a functional junior homonym of *Singhiapollis* Kar and Sah (1970). *Oroszlanyipollis*, as originally described by Góczán and Juhász (1984), is distinguished by its thicker exine and larger sexine/nexine thickness ratio.

Jusinghipollis ticoensis sp. nov.

(Fig. 4M–P; 7F–I).

2012 Angiosperm indet., Limarino et al., Fig. 6 (25).

Derivation of name. In reference to the geologic unit where the studied material comes from.

Holotype. BA Pal 6232-20-1: W44/2, Fig. 4.O–P.

Type locality. Anfiteatro de Ticó locality, Santa Cruz Province, Argentina.

Stratigraphic horizon. Anfiteatro de Ticó Formation, Baqueró Group, upper Aptian.

Diagnosis. Trichotomosulcate pollen, semitectate-reticulate. Lumina 0.6–1.3 μm in maximum diameter, subpolygonal. Muri 0.3–0.4 μm wide, narrower than lumina (index muri/lumina 0.15–0.35), sculptured by minute coni/granules that give a beaded appearance.

Description. Trichotomosulcate pollen, semitectate columellate, amb circular to subcircular. Exine microreticulate (1.6–2.7 μm thick), homobrochate. Nexine smooth (0.6–1.1 μm thick), sexine (1–1.6 μm thick) composed of club-shaped columellae, 0.6–1.3 μm in basal width, 0.28–0.67 μm apart. Lumina subpolygonal in shape (0.6–1.3 μm in maximum diameter). Muri 0.3–0.4 μm wide, narrower than lumina (index muri/lumina 0.15–0.35), sculptured by minute coni/granules (0.9–0.13 μm wide and 0.06–0.09 μm tall) that give a beaded appearance.

Dimensions. Equatorial diameter: 22(25)30 μm (81 specimens).

Remarks. It is interesting to analyze the occurrence of this aperture type. The earliest reports are from the Barremian of Southern England (Hughes, 1994) and the Aptian–lower Albian of

the Potomac Group, with doubtful designations (Doyle & Robbins, 1977; Friis et al., 1997).

In a review of Cretaceous angiosperm pollen forms, Juhász and Góczán (1985) found that pollen grains with trichotomosulcate apertures have a wide area of occurrence comprising several localities in North America and Europe, in deposits that are middle Albian to middle Cenomanian in age. More recently, reports from Gondwana have been published by Heimhofer and Hochuli (2010), who recorded three trichotomosulcate forms (*Asteropollis* spp.), present at low latitude localities of Brazil, from upper Aptian–middle Albian strata. In summary, *Jusinghipollis ticoensis* sp. nov. constitutes one of the first records of this pollen type in the Lower Cretaceous of southern South America, which is quite synchronous with other regions. However, it is important to take into account that since trichotomosulcate pollen grains have been assigned to different genera depending on the author (e.g. Dettmann, 1973; Friis et al., 1997; Heimhofer et al., 2007; among others), as was discussed above, it is very difficult to correctly address the stratigraphic distribution of these forms.

Comparison. *Singhipollis microreticulatus* Juhász & Góczán, 1985 presents smaller lumina and shorter columellae, as well as smaller diameter than *Jusinghipollis ticoensis* sp. nov. *Singhipollis vulgaris* (Groot and Groot) Juhász & Góczán, 1985 differs by having smaller diameter (17–18 μm) and irregular lumina (1–2 μm). Pollen grains attached to *Anacostia marylandensis* and *A. virginensis* (Friis et al., 1997) exhibit either trichotomosulcate or monocolpate forms. In the latter cases, they differ from *Jusinghipollis ticoensis* sp. nov. in the well-defined aperture edge and by having smaller lumina close to it. The pollen grains from the Potomac Group illustrated as aff. *Clavatipollenites* sp. 1 of Couper (1958) by Walker and Walker (1984) and as aff. *Clavatipollenites hughesii* by Doyle and Robbins (1977) are similar to our specimens, but unfortunately more detailed comparisons are not possible, since these specimens were illustrated but not described.

Genus *Lethomasites* Ward, Doyle, & Hotton, 1989.

Type species. *Lethomasites fossulatus* Ward et al., 1989.

Remarks. Ward et al. (1989) adopted a minimum size limit of 60 μm for the genus *Lethomasites*. Our specimens are close to this size, and also share the rest of the morphological characteristics, and thus are referred to this genus. Future studies using Transmission Electron Microscopy may reveal ultrastructure details that may support or refute its placement among angiosperms.

Lethomasites sp. (Fig. 5A–D; 7J–L).

Description. Monocolpate pollen grains, tectate-perforate, elongated, frequently compressed laterally or rolled up along the colpus. Colpus extending along the whole length of grain. Exine fossulate, 0.4–0.8 μm thick, perforations irregular in size and shape, fossulae curved to elongated, with grana in the floor of these perforations.

Dimensions. Long equatorial axis 49(53)56 μm , short equatorial axis 16(18)19 μm (13 specimens).

Comparison. *Lethomasites* sp. resembles *Lethomasites fossulatus* Ward et al., 1989 in being laterally compressed grains, having foveolate or fossulate exine, with grana on the floor, and tectal perforations larger in the middle of the grain and smaller or absent at the ends and on the colpus margins, and by having the margins of the colpus frequently rolled up along the colpus. However, they differ in size, as our specimens are smaller than those of *L. fossulatus*.

3.2. Angiosperm pollen assemblages

Angiosperm pollen grains were recovered from throughout the Anfiteatro de Ticó Formation, starting from the basal levels of the unit. It is noteworthy, that records show fluctuations in diversity, ranging from zero (nine samples, Fig. 2) to five morphotypes per sample (three samples, Fig. 2). The basal levels of the Anfiteatro de

Ticó Formation present scarce angiosperm pollen grains. Pteridophytic spores and gymnosperm pollen grains are also scarce, and present low diversity. An increase in diversity and abundance of angiosperms is observed starting from stratigraphically low levels of the unit, which yielded the BA Pal 6218 assemblages (Fig. 2). The association of *Clavatipollenites* type 2 in Archangelsky and Archangelsky (2013), *Jusinghipollis ticoensis* sp. nov., *Retimonocolpites* sp. D, ?*Retimonocolpites* sp. and *Lethomasites* sp. is recognized exclusively in the Anfiteatro de Ticó Formation. *Clavatipollenites* type 2 in Archangelsky and Archangelsky (2013) and *Jusinghipollis ticoensis* sp. nov. are the most abundant taxa in this unit. Two taxa, *Clavatipollenites* sp. 1 in Archangelsky and Archangelsky (2013) and *Retimonocolpites* sp. A in Llorens (2003), extend their record to the younger Punta del Barco Formation.

Clavatipollenites sp., *Retimonocolpites* sp. B in Llorens (2003) and *Retimonocolpites* sp. C are identified exclusively from the Punta del Barco Formation, while *Clavatipollenites* sp. 1 in Archangelsky and Archangelsky (2013), shared with the Anfiteatro de Ticó Formation, and *Clavatipollenites* sp. B in Llorens (2003) are the most abundant taxa in this unit. Re-examination of the materials studied by Llorens (2003, 2005) allowed the reassignment of some specimens, based on a more complete study enhanced by the recovery of new specimens. Furthermore, some assignments were made to unify previous names with the taxonomic scheme introduced by Archangelsky and Archangelsky (2013). On the other hand, the record of *Asteropollis* sp. reported for the Punta del Barco Formation by Llorens (2003; Fig. 2H) was discarded, based on re-examination of those specimens, which most certainly represent angiosperm pollen grains, but due to their poor preservation a more accurate assignment was not possible.

Recently, Archangelsky et al. (2009) analyzed angiosperm megafloreal and palynological records in central and southern Argentinean basins, recognizing three stages in their evolution in this region of Gondwana. The first stage (Stage I) included angiosperm remains from the Baqueró Group, and was dated as late Barremian–Aptian, using as a reference the age established at that time for the unit. New more accurate ages obtained for the Baqueró Group, a CA-TIMS U–Pb zircon age of 114.67 ± 0.18 Ma from the Punta del Barco and 118.23 ± 0.09 Ma from the Anfiteatro de Ticó formations (Césari et al., 2011; Perez Loínaze et al., 2013), should extend Stage I to the late Aptian. This stage is characterized by the earliest angiosperm pollen record, represented by the *Clavatipollenites* complex, while Archangelsky et al. (2009) recognized later in this stage an incipient increase in diversity of angiosperms, based on the pollen types described by Llorens (2003) from the Punta del Barco Formation. Recent studies of angiosperm pollen from the Anfiteatro de Ticó Formation (Archangelsky & Archangelsky, 2013), and new data provided here for this unit, coupled with the re-examination and reassignment of the specimens from the Punta del Barco Formation show that this incipient increase in diversity is not observed. Moreover, an impoverishment in the diversity of the angiosperm assemblage is documented in the Punta del Barco Formation, when it is compared with the angiosperm assemblages from the slightly older Anfiteatro de Ticó Formation.

4. Discussion

4.1. Taxonomic diversity

One of the most relevant issues affecting the study of the origin and early diversification of angiosperms is the fact that most of the sequences containing such ancient representatives of the group are not accurately dated, including assemblages dated using relative ages, and absolutely dated floras with ages that have a large confidence interval. As such, it is interesting to analyze the variation in diversity within the Baqueró Group stratigraphic sequence, which is accurately

dated, to calibrate the rise of the different angiosperm pollen types. Archangelsky and Archangelsky (2013) reported six angiosperm pollen types for the older Anfiteatro de Ticó Formation: four species belonging to *Clavatipollenites*, one to *Retimonocolpites*, and one to *Anacostia* pollen type, three of which are reported here as well. When our data are added, the resulting number of pollen types from the unit rises to 11, distributed among the genera *Clavatipollenites*, *Retimonocolpites*, *Anacostia* pollen type, *Jusinghipollis* and *Lethomasites*. The new record of angiosperm taxa provided in this work for the Baqueró Group reveals that the flowering plants were more diverse than previously thought during the late Aptian of Patagonia, as was previously suggested by Archangelsky and Archangelsky (2013).

Generic and specific diversity in the younger Punta del Barco Formation, at the top of the Baqueró Group, decreases more than fifty percent, with only five types recorded, referred to the genera *Clavatipollenites* and *Retimonocolpites*. The decrease in taxonomic diversity observed between the basal and upper units of the Baqueró Group (i.e. Anfiteatro de Ticó and Punta del Barco, respectively) is concordant with the decrease in diversity in gymnosperm and fern palynomorphs reported by Llorens (2012), and also observed in the megafloreal record (Limarino et al., 2012). This impoverishment of the flora is probably tied to changes in climatic and/or environmental conditions, as was previously suggested (Limarino et al., 2012).

Volcanic activity is recorded throughout the Baqueró Group (Cladera et al., 2002; Limarino et al., 2012), but reaches its maximum during deposition of the Punta del Barco Formation (Cladera & Cúneo, 2002; Limarino et al., 2012). This is evident from the recurrent and thick ash-fall deposits typical of this unit, which are especially conspicuous in its uppermost levels (De Barrio, Panza, & Nullo, 1999; Hechem & Homovc, 1987; Lesta & Ferello, 1972). This increase in volcanic activity was probably responsible of the impoverishment of the flora, including angiosperm pollen grains, recorded in the Punta del Barco Formation, when compared with the diversity in the Anfiteatro de Ticó Formation.

4.2. Botanical affinities

4.2.1. *Clavatipollenites* spp.

Chloranthaceae are a small family that currently includes four genera: *Ascarina*, *Chloranthus*, *Hedyosmum* and *Sarcandra*. *Chloranthus* and *Sarcandra* pollen grains have smooth muri (Eklund et al., 2004), and most species of that taxa include polyforate forms, but the former genus also produces polycolpate grains. On the other hand, *Ascarina* and *Hedyosmum* have pollen grains with supramural sculpture (Eklund et al., 2004), both have a monosulcate aperture, which is star-shaped with 4–6 branches in the latter genus, while the aperture has trichotomosulcate variants in the former (Doyle & Endress, 2014; Eklund et al., 2004; Martínez, Madriñán, Zavada, & Jaramillo, 2013; Walker & Walker, 1984).

Clavatipollenites pollen grains, recorded from the Early Cretaceous to the Quaternary, are interpreted as related to the modern family *Chloranthaceae* (Chapman, 1987; Doyle, Van Campo, & Lugardon, 1975; Walker & Walker, 1984). Furthermore, it has been compared with *Ascarina* since Couper (1958) gave the first descriptions of the fossil genus. Reticulate pollen grains referred to the genus *Clavatipollenites*, found in situ onto the stigmatic surface of the small uniovulate fruit *Couperites mauldinensis* were recovered by Pedersen, Crane, Drinnan, and Friis (1991), from lower Cenomanian Potomac Group deposits. The relationship of *Couperites* with *Chloranthaceae* was suggested tentatively; however, based on phylogenetic analyses, Doyle and Endress (2014) considered this relationship as uncertain. According to these authors, affinities with *Chloranthaceae* of all dispersed pollen grains assigned to *Clavatipollenites* are not necessarily applicable, pointing out that this genus of pollen

grains could be systematically heterogeneous, since they exhibit many plesiomorphic features. *Clavatipollenites* sp. 1 in Archangelsky and Archangelsky (2013) and *Clavatipollenites* sp. 2 in Archangelsky and Archangelsky (2013) may be assigned to *Chloranthaceae* due to the presence of supramural sculpture. Doyle and Endress (2014) pointed out that this character evolved between stem *Chloranthaceae* (such as *Canrightia* and *Zlatkocarpus*) and the crown group, and later reverted in the *Sarcandra* + *Cloranthus* clade. These results suggest that the C. sp. 1 in Archangelsky and Archangelsky (2013) and C. sp. 2 in Archangelsky and Archangelsky (2013) could be potentially related to *Ascarina*, but also to other stem *Chloranthaceae* more derived than *Canrightia* and *Zlatkocarpus*.

Clavatipollenites sp. possess a mixture of features distributed among (but not exclusive to) several *Chloranthaceae* genera, such as smooth muri (as in *Chloranthus* and *Sarcandra*), and monocolpate aperture (a plesiomorphic feature also observed in *Ascarina*), and thus is difficult to suggest clear botanical affinities. It may represent an extinct lineage within *Chloranthaceae*, or may not be related to this family at all.

4.2.2. *Jusinghipollis ticoensis* sp. nov

Fossil pollen grains with trichotomosulcate apertures recognized in the late Early Cretaceous are usually referred to dicotyledons, because this type of aperture occurs in *Chloranthaceae* (*Ascarina*) and in some magnoliids. However, monocotyledonous affinity is also possible (Harley & Baker, 2001), since trichotomosulcate pollen grains are recorded in several taxa, occurring in combination with monosulcate grains. Exceptionally, species of *Acrocomia* and *Bactris* of the subfamily Arecoideae within the *Arecaceae* produce only trichotomosulcate grains (Harley, 2006). *Jusinghipollis* is considered for some authors to be similar to pollen grains of the *Arecaceae* (Harley & Baker, 2001). However, Harley (2006) suggested that due to its small size it probably represents an early dicotyledon. The exine sculpture would also be consistent with monocotyledonous or dicotyledonous affinities.

4.2.3. *Lethomasites* sp.

Lethomasites fossulatus Ward et al., 1989 is a questionable angiosperm pollen grain, and 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 the fossils (Doyle & Hotton, 1991; Ward et al., 1989). In addition, *Lethomasites* has some features also present in the bennettitalean lineage (Crepet & Nixon, 1994).

4.2.4. *Retimonocolpites* spp.

The genus *Retimonocolpites* lacks well-defined botanical affinities, except for besides being angiospermous in origin, and probably represents a polyphyletic collection of non-closely related taxonomic entities, which are difficult to segregate into more natural groups (Friis et al., 2011).

4.3. Comparison with other palynofloras

A comparison of Early Cretaceous angiosperm pollen assemblages made using multivariate statistic methods (Fig. 3) shows the greatest similarities between the Punta del Barco and Anfiteatro de Ticó formations with the Argentinian Pozo D-129 Formation (Aptian), and the Australian *Cyclogranisporites hughesii* (upper Barremian–Aptian) and *Crybelosporites striatus* (lower Albian) zones (Burger, 1990; Dettmann, 1973, 1994). Strong similarities are also observed with the Ranquiles (=Quili Malal Member of the Rayoso Formation, Aptian), and La Cantera (upper Aptian) formations from Argentina, as well as with the Gachetá Formation

(Aptian), Moyén level (lower Aptian) and lower level of Villaviciencio locality (lower Aptian) from Colombia, and with the lower part of the Zone I from the Potomac Group (United States). These results reinforce previous observations made by Romero and Archangelsky (1986), who are based on the megafloreal remains of the Anfiteatro de Ticó Formation, noted that the angiosperm leaves of this unit shared individual characteristics with leaves described for the Potomac Group (Doyle & Hickey, 1976). Consistent with this, the angiosperm pollen assemblages studied here have important similarities with the lower part of the Zone I of the Potomac Group (United States, Doyle & Robbins, 1977), dated as Aptian by Hochuli et al. (2006) and Aptian-early Albian by Doyle and Endress (2014).

Similar result were obtained by Perez Loinaze et al. (2015) with basis on a study of angiosperm pollen grains from the Albian Kachaiké Formation (Austral Basin, Argentina), who noted similarities between these palynofloras and others from Australia and the Potomac Group, which were located in a similar paleolatitude.

The Brazilian palynofloras from the Río da Batateira (upper Aptian), Crato (upper Aptian), and Santana (lower Albian) formations (Heimhofer & Hochuli, 2010) are coeval with the palynological assemblages here studied but present lower similarity values due to the presence of eudicots at equatorial areas during the Aptian, where the Brazilian territories were located, while records of this group of plants appear near the Aptian–Albian boundary at middle latitudes.

5. Conclusions

A new detailed study of the angiosperm pollen grains of the Baqueró Group is presented, including the revision of previously published materials from the Punta del Barco Formation, as well as new samples from the Anfiteatro de Ticó and Punta del Barco formations. Ten pollen types are recognized in this work, comprising four genera, i.e., *Clavatipollenites*, *Retimonocolpites*, *Jusinghipollis* and *Lethomasites*. Among these, the first three are conclusively referred to angiosperms, whereas the later (*Lethomasites*) is referred to this group, but its possible affinities with other non-angiosperm plant groups are discussed.

The species *Retimonocolpites* sp. C, *Retimonocolpites* sp. D, *Jusinghipollis ticoensis* sp. nov. and *Lethomasites* sp. are reported for the first time for this unit. *Clavatipollenites* sp. 1 Archangelsky and Archangelsky (2003), originally described from the Anfiteatro de Ticó Formation, is here recognized also in the younger Punta del Barco Formation. Conversely, *Retimonocolpites* sp. A in Llorens (2003), originally described from the Punta del Barco Formation, is recorded in the Anfiteatro de Ticó Formation as well. These results increase our knowledge of the taxonomic diversity of angiosperms during the late Aptian, which was higher than previously thought.

The study of two new fossiliferous levels and the re-examination of the palynofloras studied by Llorens (2003, 2005) from the Punta del Barco Formation led to rejection of the presence of the genus *Asteropollis* in this unit, and the referral of some specimens described by Llorens (2003) to other genera.

The reassessment of some of the taxa described by Llorens (2003, 2005) from the Punta del Barco Formation and the study of a new sample from the same unit, reveal a less diverse angiosperms association in this unit, when compared with the Anfiteatro de Ticó Formation assemblages. This decrease in diversity is probably the result of the increased volcanic activity recorded in the upper part of the Baqueró Group, which not only affected angiosperms but the whole floristic community.

Previous works (Llorens, 2003, 2005) reported an increase in angiosperm taxa in the Punta del Barco Formation, when compared with other slightly older palynofloras (e.g. Anfiteatro de Ticó Formation), being this the basis for postulating an incipient increase in

angiosperm diversity in the Upper Stage I of angiosperm evolution in the southernmost region of South America (Archangelsky et al., 2009). Even if it is clear that worldwide angiosperm diversity increased in the late Aptian (when compared with older assemblages), the results of this work do not support this increase from the base to the top of the Baqueró Group (i.e. Anfiteatro de Ticó to Punta del Barco palynofloras), probably reflecting local dynamics of the community affected by harsh environmental conditions.

The new species *Jusinghipollis ticoensis* sp. nov. represents one of the oldest records of trichotomosulcate forms from accurately dated stratigraphical provenance. This new taxon also extends the geographical distribution of Early Cretaceous trichotomosulcate pollen grains to southern South America.

The morphological diversification of angiosperm pollen grains in late Aptian middle latitudes shows only one major morphological group (uniaperturate), with a broad variety of morphological patterns in both aperture development and wall structure.

A comparison between Early Cretaceous angiosperm pollen assemblages made using multivariate statistical methods show strong similarities between the Baqueró Group assemblages and other coeval units from Argentina, Australia and United States, which were located in a similar paleolatitude.

This new study of the palynological content of the Baqueró Group, with precise age estimates based on U–Pb geochronology, contributes to reconstructing the early history of flowering plants, and allows a better characterization of the emerging picture of early angiosperms.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.cretres.2015.07.019>

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