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## APTIAN ANGIOSPERM POLLEN FROM THE TICÓ FLORA PATAGONIA, ARGENTINA

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Six angiosperm pollen types studied with SEM are recorded in the Cretaceous (early Aptian) Ticó flora on the basis of material recovered from two localities: Anfiteatro de Ticó and Bajo Tigre. *Clavatipollenites* dominates, with four types described. The other two types, based on single specimens, were referred to *Retimonocolpites* and to the *Anacostia* type. Comparisons are made with similar species found in other Cretaceous paleofloristic regions and with other Aptian pollen assemblages from Patagonia. The chloranthaceous affinity of *Clavatipollenites* agrees with known paleobotanical, sedimentological, and paleoclimatical data obtained for the same fossiliferous horizons of the Anfiteatro de Ticó Formation studied here. During the early Aptian, a warm and humid paleoclimatic belt extended to latitudes greater than 60°S in SW Gondwana. This belt is known to have persisted until the late Aptian in southern Patagonia. The angiosperm pollen variety is further underscored by fossil leaves found in two of the horizons studied here, suggesting that angiosperms may have existed during the Barremian in SW Gondwana (Patagonian Province).

**Keywords:** angiosperms, Aptian, Cretaceous, Patagonia, pollen, Ticó flora.

### Introduction

During the Early Cretaceous, especially the Barremian and early Aptian, angiosperms began to differentiate (Friis et al. 2011). In some regions of the Northern Hemisphere, they have more or less continuous stratigraphic records that are based on leaves, mesofossils (including fertile structures), or microfossils (mainly pollen). At present, the Potomac sequence in North America (Doyle 1992) and the Lusitanian Basin of Portugal (Heimhofer et al. 2007; Friis et al. 2010a, 2010b) are probably the best known Early Cretaceous sequences bearing angiosperms. Pre-Aptian angiosperm records also have been reported sporadically from other regions, including Israel (Brenner 1996), England (Hughes 1994), Morocco (Gübeli et al. 1984), and Egypt (Schrank and Mahmoud 2002).

In the Southern Hemisphere, mid-Cretaceous strata occur widely. In some regions, mainly in southern South America, angiosperm remains were reported 100 yr ago (Halle 1913). In the past few years, several articles have been devoted to the study of mid-Cretaceous angiosperm leaves and pollen found in different areas of Patagonia (Prámparo 1999; Passalía et al. 2003; Cúneo and Gandolfo 2005; Vallati 2006; Del Fueyo et al. 2007; Archangelsky et al. 2009). In particular, the rich fossil flora from the Anfiteatro de Ticó Formation of the Baqueró Group (the Ticó flora) has yielded the oldest (early Aptian) angiosperm remains in that region. Leaves (Romero and Archangelsky 1986; Passalía et al. 2003), dispersed pollen (Archangelsky and Gamero 1966), or pollen found inside pollen sacs (Archangelsky and Taylor 1993) have been described. The pollen was referred to the genus *Clavatipollentes* Couper

(1958) and considered to be the oldest known record of angiosperms in Patagonia (Archangelsky et al. 2009).

In this article, we present new angiosperm pollen types from the Ticó flora to show that during the early Aptian in Patagonia, this group was more diverse than previously suspected. This result is coincident with data from other regions, and it also gives support to previous information on Patagonian isolated borehole records of probable pre-Aptian angiosperms in the Springhill Formation of the Austral Basin (Archangelsky and Archangelsky 2004; Quatrocchio et al. 2006). The observation of pollen with SEM proves to be valuable in better defining morphological characters that are not or are badly seen with LM. This article is a new step in this line of investigation of early Cretaceous angiosperm pollen from Patagonia.

### Material and Methods

The material was collected at two localities where the Anfiteatro de Ticó Formation is exposed: (1) Anfiteatro de Ticó and (2) Bajo Tigre (Cladera et al. 2002, figs. 1, 2, 4; see also Del Fueyo et al. 2013, fig. 1). Three fossiliferous horizons belong to the Bajo Tigre locality, namely, BTO (*Otozamites*), BTA (angiosperm leaves), and BTG (*Ginkgoites*). Two horizons correspond to the Ticó Amphitheatre, TH (*Ticoa harrisii*) and TW (*Williamsonia*). The precise location of these horizons may be found in the study by Cladera et al. (2002, fig. 3, left column [plant signs] for BTA at base, BTO and BTG at the top). Figure 5, left column (Ticó Amphitheatre section), of the same publication (Cladera et al. 2002) shows the two plant horizons studied (i.e., TH and TW). Radiometric data obtained for the BTG horizon indicate an early to mid-Aptian age of  $118.56 \pm 1.40$  Ma (Corbella 2001; Limarino et al. 2012).

Standard techniques (Gamero and Cárdenas 1980) were used to extract the organic residue from the sediments (i.e.,

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preparation with HCl and HF). The residues were sieved through 10- and 25- $\mu\text{m}$  meshes, mounted on stubs for SEM analysis, and coated with Au/Pd. A Philips XL 30 photomicroscope at the Argentine Museum of Natural Sciences was used for observation and image capture. All SEM stubs are lodged in the paleobotanical collection of the same Museum (BA Pb MEB). The morphological terminology of Punt et al. (2007) is followed in this article.

## Results

### *Description of the Material*

#### *Clavatipollenites Couper 1958*

The specimens described here agree with the original diagnosis of the genus. The grains are tectate or semitectate, columellate, and microreticulate. The species of *Clavatipollenites* described have been characterized mainly by the shape of the apertures and the sexine elements, especially the size of lumina and muri: a ratio (index number) and the thickness of muri divided by the thickness of lumina proved to be a useful tool to differentiate *Clavatipollenites* sp. 1 from *Clavatipollenites* sp. 2. The sulcus is also variable in shape, having irregular to well-defined margins. The supramural ornamentation was also a useful character to define some types. At this stage of investigation, we have avoided specific diagnoses until more material is studied to better define key characters and their variability.

#### *Clavatipollenites* sp. 1 (Figs. 1, 2)

*Description.* The amb of this type is circular (20 specimens) to subcircular-oval (14 specimens). The equatorial diameter is 19–27  $\mu\text{m}$  (35 specimens). The sulcus is up to 16.4  $\mu\text{m}$  long and very variable in shape and size, from subrectangular (fig. 1*b*, 1*c*), rarely square (fig. 1*d*), to elongate (fig. 1*c*, 1*e*, 1*f*). The sulcus margins are normally irregular (zigzag), with projecting loose reticula, columellae, and capita (and possible Übisch bodies; fig. 1*c*, 1*e*). Capita may be concentrated along the sulcus margins (fig. 1*f*). Some specimens show a poorly defined area (leptoma), ornamented with remnants of sexine elements (fig. 1*d*). The exine is semitectate, columellate, and microreticulate (fig. 1*a*). Columellae are club shaped, 0.15–0.41  $\mu\text{m}$  wide and up to 0.95 tall (including capita). They are closely arranged on a solid, up to 0.62- $\mu\text{m}$ -thick nexine, separated by a distance usually equal to their width. The nexine is not visibly differentiated into separate levels. The capita are normally rounded to slightly elongate. They expand laterally and fuse to form muri 0.15–0.52  $\mu\text{m}$  wide with slightly sinuous margins (fig. 2*c*, 2*d*). The muri are as wide as or wider than lumina (index, 0.3–0.6; fig. 2*e*). The lumina of the microreticulum are commonly of two types: circular-polygonal, isodiametric (0.15–0.79  $\mu\text{m}$  wide) to linear-elongate (up to 1.05  $\mu\text{m}$ ). Supramural ornament is composed of one to two series of minute coni/granules (0.03–0.07  $\mu\text{m}$  wide and 0.05–0.1  $\mu\text{m}$  tall) that may fuse to give a beaded appearance (fig. 2*c*, 2*e*). Separation between ornament units is usually less than their basal width. A few broken specimens show the nexine with a smooth inner surface (fig. 2*a*, 2*b*). Regular rounded to oval holes through the nexine reveal the columella bases (fig.

2*b*, 2*f*). The margins of these holes are marked by compact and regular round to oval depressed incisions probably caused by some kind of microorganism; the bases of the exposed columellae also show concave incisions (fig. 2*f*).

*Studied material.* Bajo Tigre: horizons BTG, BA Pb MEB 374; BTO, BA Pb MEB 384, 393; BTA, BA Pb MEB 366, 367.

*Comments.* Some specimens show dispersed capita distributed over the surface, sulcal edges, and membrane; a few may well correspond to remnants of Übisch bodies (fig. 1*d*). The relationship between the Übisch bodies and the heads of the columellae in a *Clavatipollenites* from Ticó has been clearly shown in TEM sections (Archangelsky and Taylor 1993, figs. 16, 17).

#### *Clavatipollenites* sp. 2 (Figs. 3, 4a–4c)

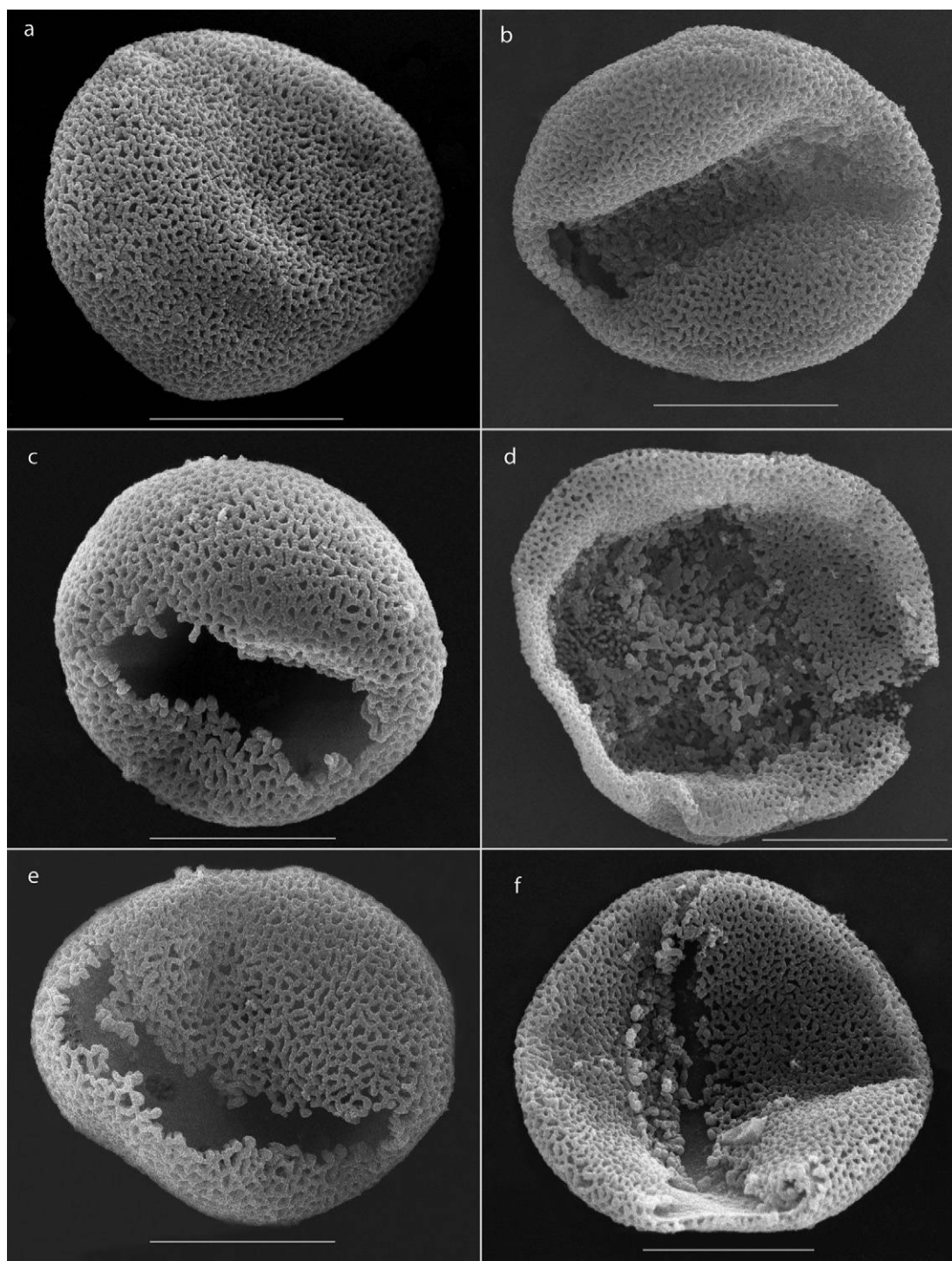
*Description.* The amb of this type is oval (17 specimens) to circular (13 specimens). The equatorial diameter is 19–26  $\mu\text{m}$  (30 specimens). The sulcus is elongate/rectangular to oval, rarely subcircular, up to 17  $\mu\text{m}$  long. It may be widely opened (fig. 3*d*) with irregular (zigzag) margins (figs. 3*b*, 4*a*) or closed with straight involute sides (fig. 3*c*). Some specimens show a collapsed area (leptoma) that is sculptured with dispersed sexine elements (fig. 3*d*). The exine is semitectate, columellate, and microreticulate (fig. 3*a*). Columellae are club shaped, 0.10–0.23  $\mu\text{m}$  wide and up to 1  $\mu\text{m}$  tall (including capita). They are closely disposed on a solid, up to 0.5- $\mu\text{m}$ -thick nexine and separated by a distance either equal to or less than their width (fig. 4*c*). The capita expand laterally and fuse to form muri 0.14–0.37  $\mu\text{m}$  wide and slightly sinuous margins. The muri are as wide as or thinner than lumina (index, 0.09–0.3). The lumina of the microreticulum are of two main types: circular-polygonal, isodiametric (0.21–0.89  $\mu\text{m}$  wide) to linear-elongate (up to 1.58  $\mu\text{m}$ ). The supramural ornament is composed of one to two series of minute coni/verrucae (0.1–0.2  $\mu\text{m}$  wide and 0.05–0.1  $\mu\text{m}$  tall) that may fuse to give a beaded appearance (figs. 3*f*, 4*c*). Separation between ornament units is usually less than or equal to their basal thickness.

*Studied material.* Bajo Tigre, horizons BTA: BA Pb MEB 366, 367; BTO: BA Pb MEB 384, 393; BTG: BA Pb MEB 374, 375.

*Comments.* The sexine is often separated from the nexine (fig. 3*e*, 3*f*), and when broken, it shows the naked nexine, which may support randomly distributed columella bases.

#### *Clavatipollenites* sp. 3 (Fig. 5)

*Description.* The amb of this type is typically oval (12 specimens) with an equatorial diameter of 19–30  $\mu\text{m}$ . The sulcus is elongate/rectangular to oval, up to 22  $\mu\text{m}$  long. It may be widely opened, showing irregular/zigzag margins (fig. 5*d*) with loosely disposed sexine elements and round bodies, or may have straight involute sides (fig. 5*a*). Some specimens show a collapsed area (leptoma) that is sculptured with dispersed sexine elements (fig. 5*c*). The exine is semitectate, columellate, and finely reticulate. Columellae are club shaped (fig. 5*e*, 5*f*), 0.05–0.29  $\mu\text{m}$  wide and up to 1  $\mu\text{m}$  tall (including capita of up to 0.56  $\mu\text{m}$ ). They are closely disposed on a solid and smooth, up to 0.5- $\mu\text{m}$ -thick nexine (fig. 5*f*) and separated by

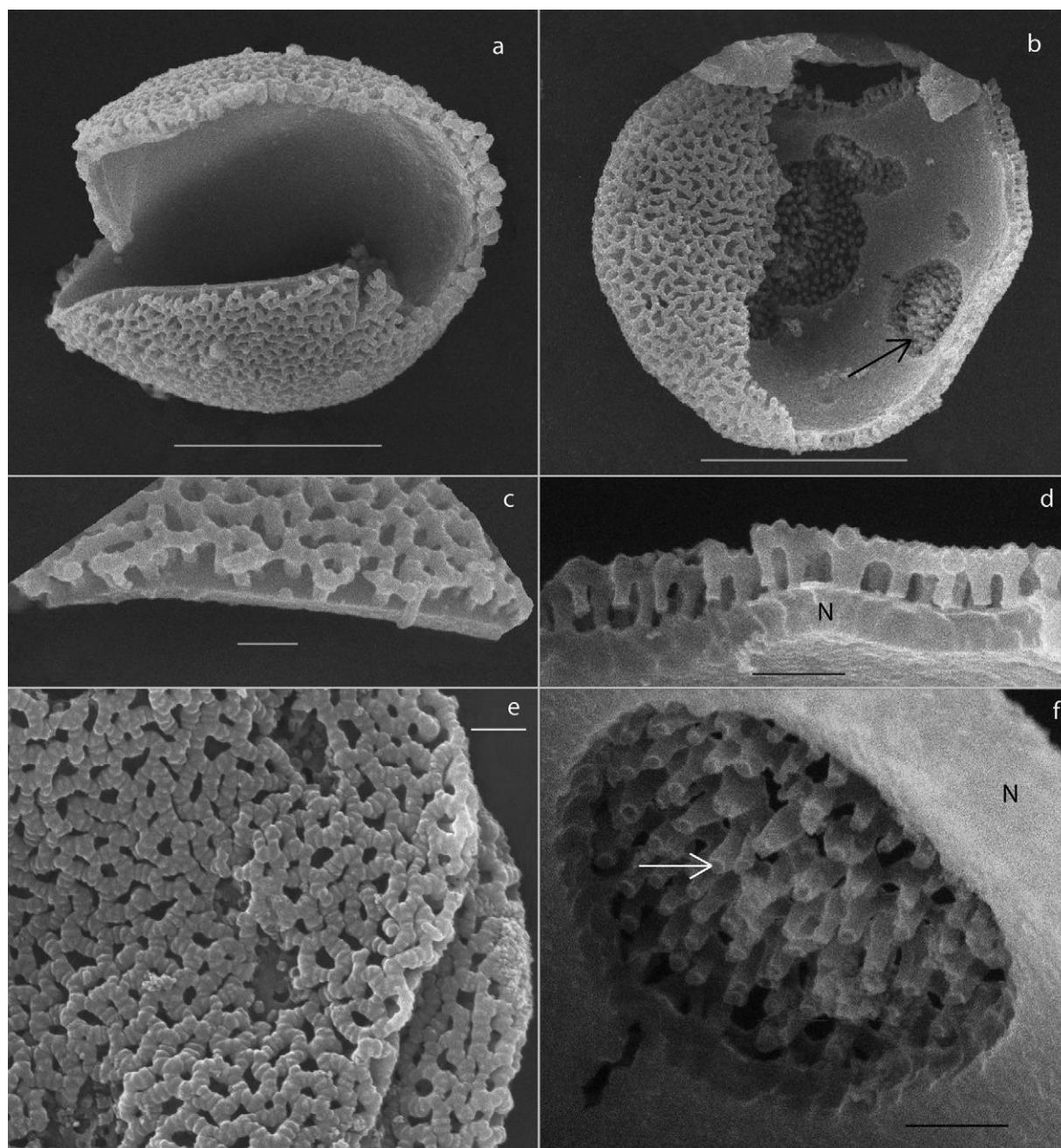


**Fig. 1** SEM views of *Clavatipollenites* sp. 1. *a*, Nonaperturate side of grain. *b*, Sulcus with subrectangular shape. *c*, Rectangular aperture with loose columellae projecting from sulcus margin. *d*, Sulcus of square shape with remnants of sexine elements on membrane. *e*, Sulcus with irregular margins and projecting loose reticula. *f*, Elongate sulcus with capita/orbicules concentrated along margins. *a*, *b*, BTA 367. *c*–*f*, BTO 384. Scale bars = 10  $\mu\text{m}$ .

a distance usually equal to or more than their width. The capita expand laterally and fuse to form muri 0.05–0.31  $\mu\text{m}$  wide with sinuous margins. The muri are much thinner than lumina (index, 0.08–0.19) and up to 0.26  $\mu\text{m}$  high (fig. 5*a*,

5*c*). The lumina of the fine reticulum are of two main types: circular-polygonal, isodiametric (0.25–1  $\mu\text{m}$  wide) to linear-elongate (up to 2.35  $\mu\text{m}$ ). A few small granules may be present inside the lumina. Supramural ornament is composed of





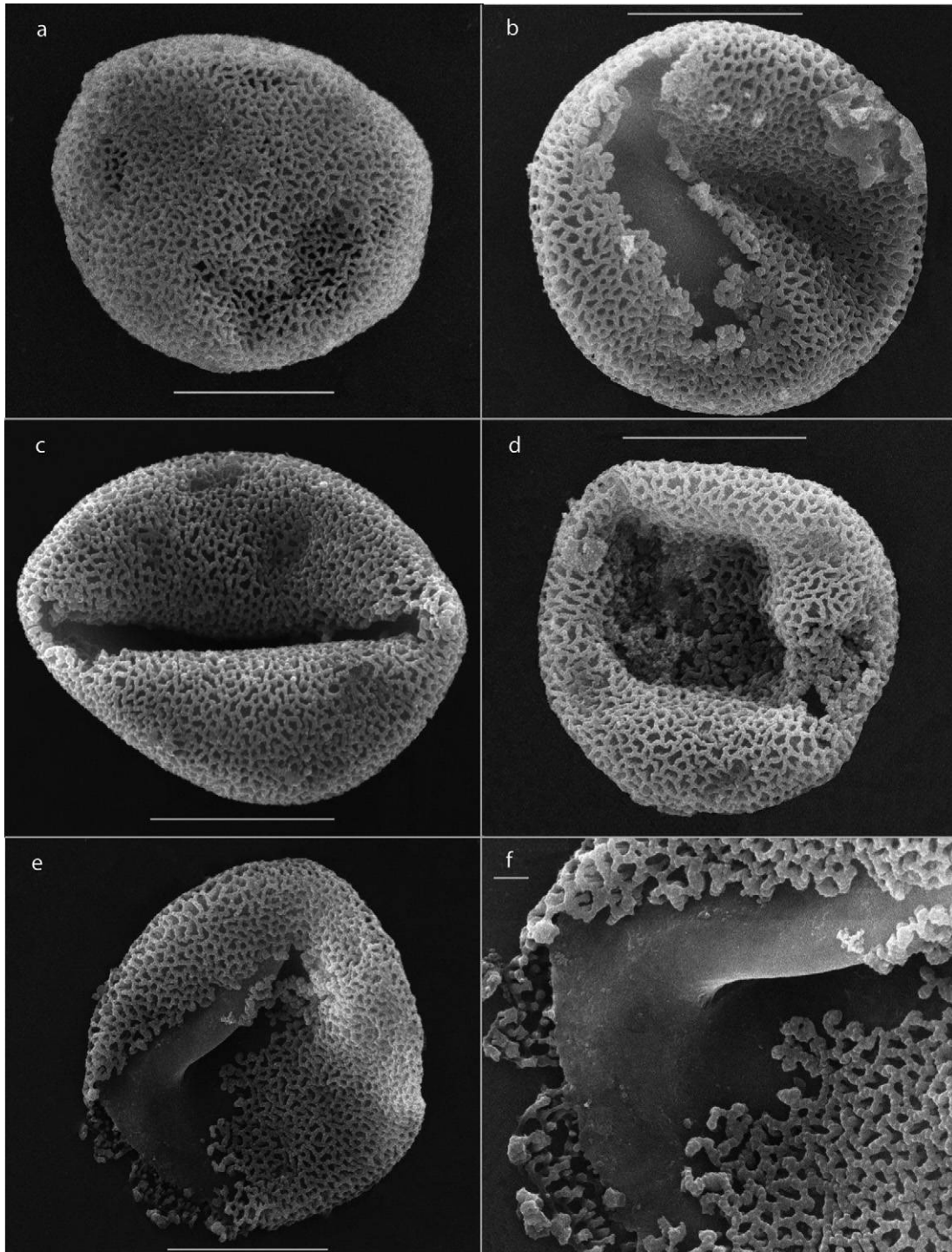
**Fig. 2** SEM views of *Clavatipollenites* sp. 1. *a*, Broken specimen showing solid nexine with smooth inner surface. *b*, Broken specimen showing inner holes through nexine (arrow) and uncovered columellae bases. *c*, Oblique section of exine showing basal nexine supporting columellae and reticulum with ornamented muri. *d*, Transverse section of *b*, showing thick nexine (N) and details of laterally fused, club-shaped columellae. *e*, Detail of beaded appearance of supramural ornamentation. *f*, Detail of *b*, showing nexine (N) with presumed incisions by microorganisms (bottom left margin of hole) and concave bases of columellae (arrow). *a*, *c*, BTO 393. *b*, *d*, *f*, BTO 384. *e*, BTA 366. Scale bars = 10  $\mu\text{m}$  (*a*, *b*), 1  $\mu\text{m}$  (*c*–*f*).

one to two series of minute conigranules (0.05–0.15  $\mu\text{m}$  wide and 0.05–0.15  $\mu\text{m}$  tall) that may fuse to give a typical beaded appearance (fig. 5*e*). Separation between ornament units is usually less than or equal to their basal thickness. In some specimens, the sexine easily separates from the nexine layer, leaving large bare areas with only a few dispersed granules, probably corresponding to bases of columellae (fig. 5*b*).

*Studied material.* Bajo Tigre, horizon BTO: BA Pb MEB 384, 393; BTA 366, 367; BTG 374, 375; Ticó Amphitheatre: TH, MEB (not numbered).

#### *Clavatipollenites* sp. 4 (Fig. 6*a*–6*d*)

*Description.* Pollen grains with a typical circular amb, 20–23  $\mu\text{m}$  in equatorial diameter (fig. 6*b*). Sulcus poorly de-

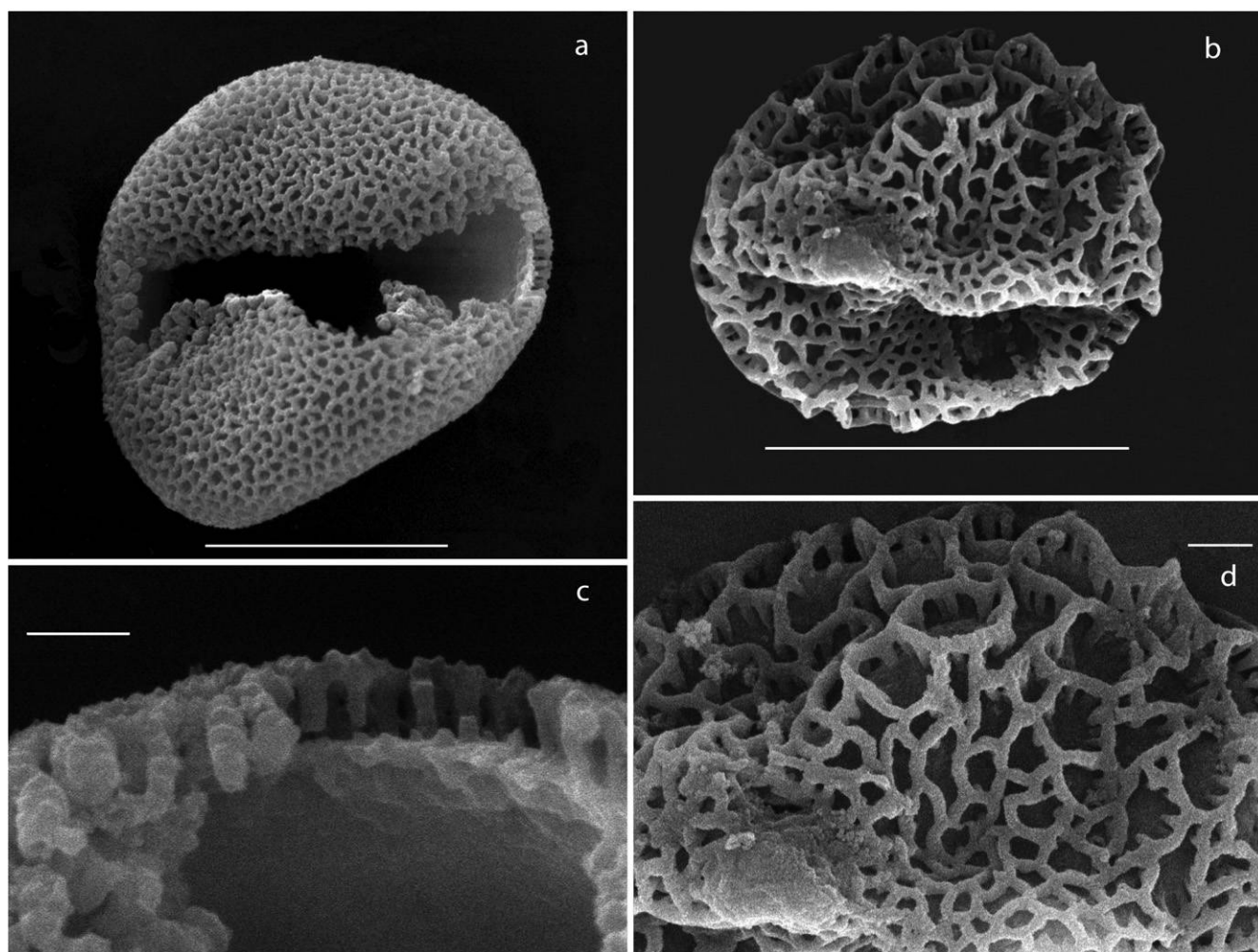


**Fig. 3** SEM views of *Clavatipollenites* sp. 2. *a*, Nonaperturate side of grain. *b*, Sulcus with irregular (zigzag) margin. *c*, Grain of oval amb and long sulcus with straight involute sides. *d*, Grain with subrhomboidal sulcus and membrane sculptured with loose sexine elements. *e*, Grain showing sexine partly separated from smooth nexine. *f*, Detail of grain of *e*. Note smooth nexine supporting partially loose sexine. *a*, *c*, BTO 384. *b*, *d*, BTG 375. *e*, *f*, BTA 366. Scale bars = 10  $\mu\text{m}$  (*a–e*), 1  $\mu\text{m}$  (*f*).

veloped, showing as a subcircular to subsquare depressed area (leptoma) sculptured with remnants of sexine elements (columellae or reticulum fragments; fig. 6*a*). The nexine is smooth (fig. 6*d*) and supports a semitectate, columellate/reticulate sex-

ine. Columellae are cylindrical, slightly expanded distally, 0.23–0.5  $\mu\text{m}$  wide and up to 0.73  $\mu\text{m}$  high. They are separated by spaces equal to or wider than their width. The reticulum has delicate, slightly sinuous muri 0.2–0.5  $\mu\text{m}$  wide and round to





**Fig. 4** *a, c*, SEM views of *Clavatipollenites* sp. 2. *a*, Extended and open sulcus with irregular (zigzag) margins. *c*, Transverse section of the exine showing details of sexine and nexine. Note shape of columellae with laterally fused capita and supramural beaded ornament. *b, d*, *Retimonocolpites* sp. *b*, Heterobrochate grain with an extended involute sulcus. *d*, Detail of *b* showing the reticulum with two types of lumina and cylindrical columellae. Note the lack of supramural ornament. *a, c*, BTO 384. *b, d*, BTA 366. Scale bars = 10  $\mu\text{m}$  (*a, b*), 1  $\mu\text{m}$  (*c, d*).

polygonal or elongate lumina 0.9–2.2  $\mu\text{m}$  wide (fig. 6c). Reduced areas with almost continuous tectum are present in some specimens (fig. 6d). The tectum is 0.5–0.7  $\mu\text{m}$  thick. Isolated small grains (probably aborted bases of columellae) are present inside some lumina (fig. 6d). The muri/lumina index varies from 0.11 to 0.22  $\mu\text{m}$ . The supramural ornament is composed of one series of coni or spines 0.14–0.2  $\mu\text{m}$  wide at the base and up to 0.4  $\mu\text{m}$  tall (fig. 6c). Some specimens show a thin longitudinal ridge connecting the bases of the supramural elements (fig. 6c).

*Studied material.* Four specimens. Ticó Amphitheatre, TW, BA Pb MEB 376; Bajo Tigre, BTO BA Pb MEB 384, BTP BA Pb MEB 386.

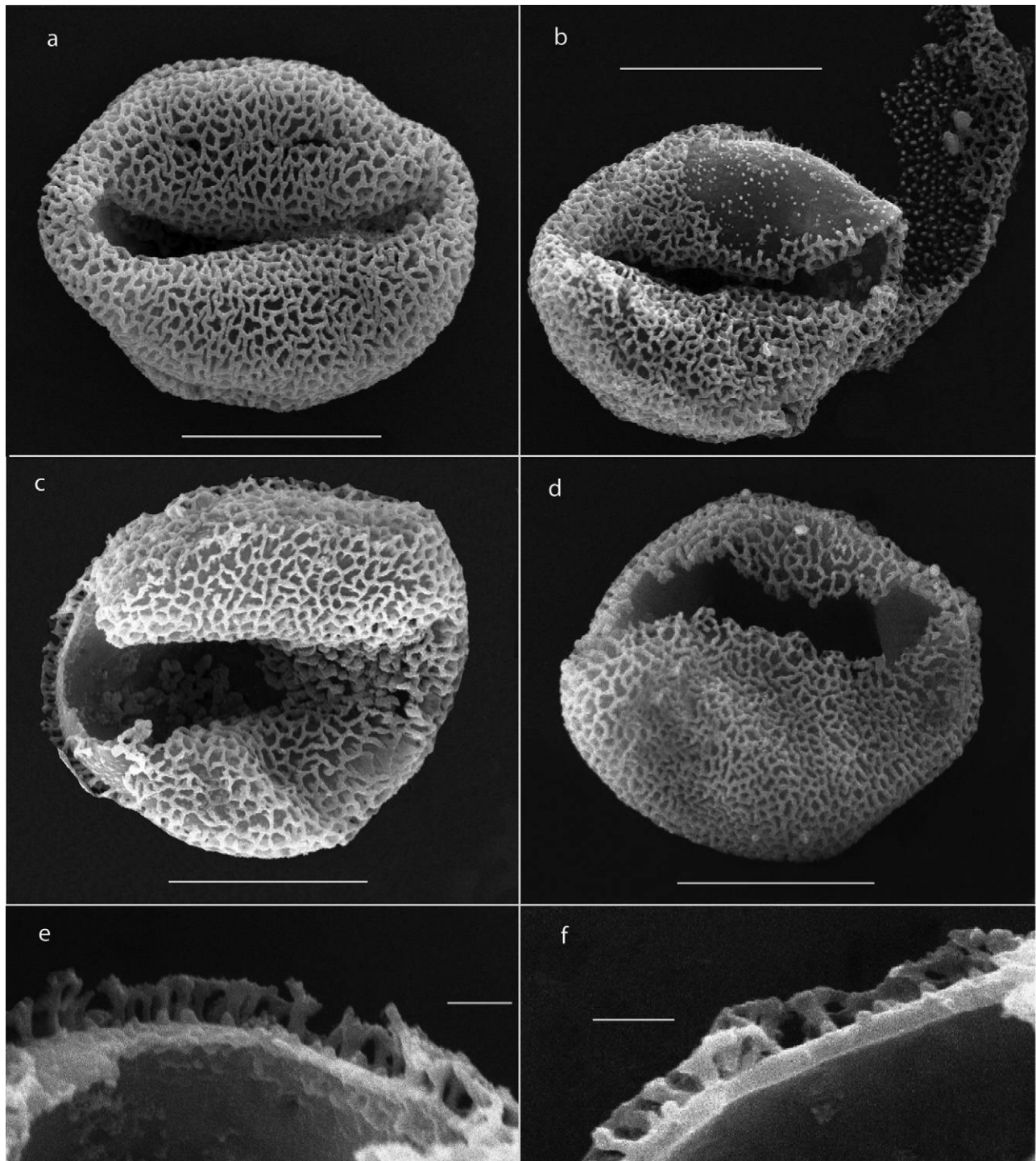
#### *Retimonocolpites* Pierce 1961

We use here *Retimonocolpites* for pollen with both homobrochate and heterobrochate reticula. This type of pollen is found in dicots and monocots and therefore has little systematic

significance. Considering that some types described in the literature are similar to our fossil, comparisons with material found in other regions are made at the generic level.

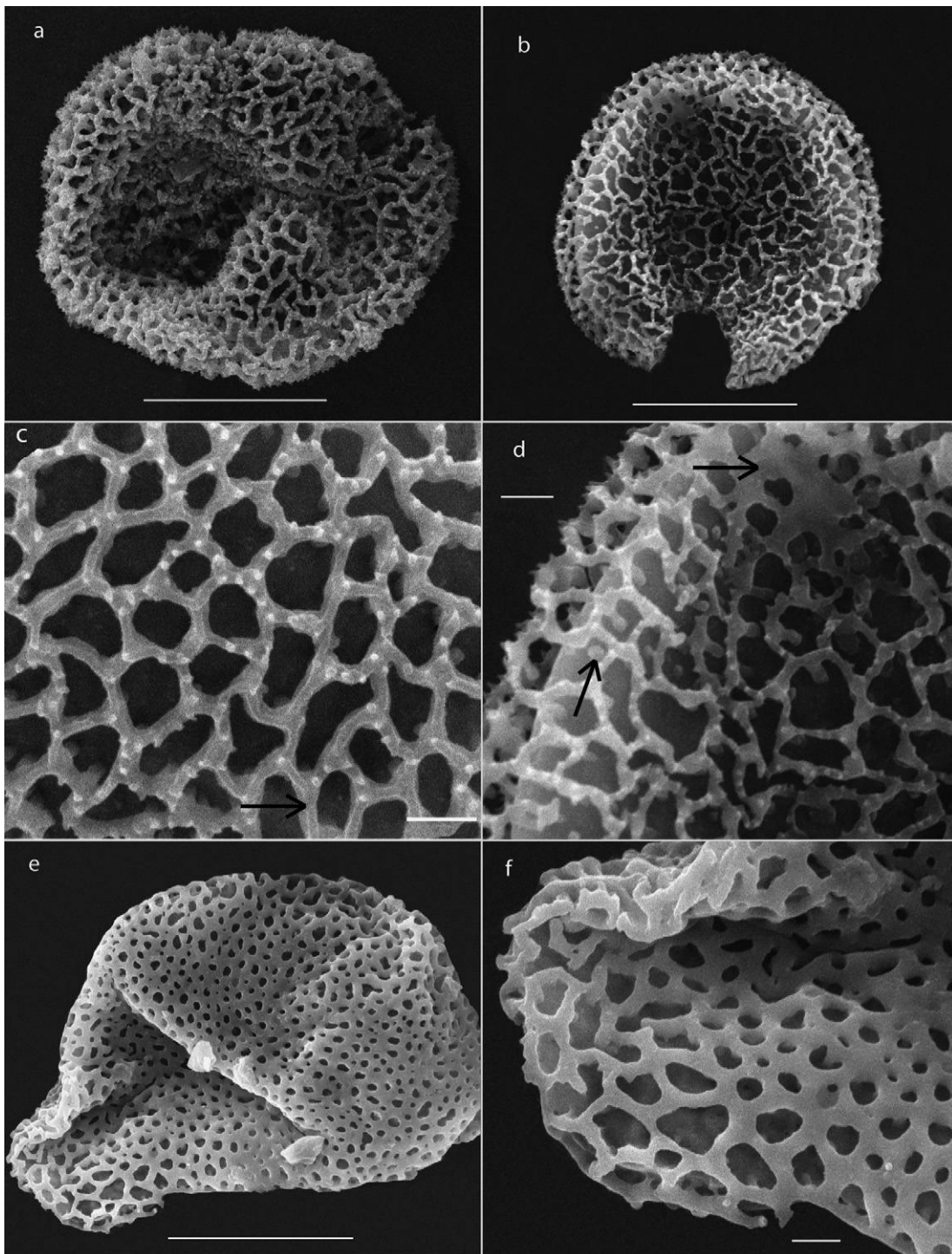
#### *Retimonocolpites* sp. (Fig. 4b–4d)

*Description.* Only one specimen of this small pollen type was found. The amb is elliptical-subcircular with a maximum diameter of 13.2  $\mu\text{m}$ . The sulcus extends for almost the total length of the grain and has an involute margin (fig. 4b). The nexine is smooth, 0.21  $\mu\text{m}$  thick, supporting a semitectate, columellate, and reticulate sexine. The fine reticulum has two kinds of lumina (fig. 4d): (1) small, isodiametric, and 0.1  $\mu\text{m}$  in diameter, concentrated along the sulcus margin; and (2) large, subpolygonal, up to 2  $\mu\text{m}$  wide, developed at the equator and proximal half of the grain. Columellae are cylindrical, slightly expanded distally, 0.16–0.24  $\mu\text{m}$  thick and up to 0.45  $\mu\text{m}$  tall, separated by spaces smaller or equal to their width (fig. 4d). They support a tectum 0.28  $\mu\text{m}$  thick. Muri



**Fig. 5** SEM views of *Clavatipollenites* sp. 3. *a*, Grain with elongated sulcus and straight involute sides. *b*, Grain showing sexine separated from nexine. Note dispersed granules on nexine, probably partly representing bases of columellae. *c*, Specimen showing collapsed apertural area of exine (leptoma) and part of sculptured membrane. *d*, Grain with elongated sulcus and irregular zigzag margins. *e*, Almost transverse section of exine of *c* with typical club-shaped columellae, laterally expanded capita, and supramural ornament. *f*, Specimen showing oblique view of solid and internally smooth nexine and columellae supporting semitectate sexine. *a*, BTA 367. *b*, *c*, *e*, *f*, BTA 366. *d*, BTO 393. Scale bars = 10  $\mu\text{m}$  (*a-d*), 1  $\mu\text{m}$  (*e*, *f*).





**Fig. 6** *a-d*, SEM views of *Clavatipollenites* sp. 4. *a*, Specimen with poorly developed subsquare aperture (leptoma) and sculptured membrane. *b*, Grain with typical circular amb. Note nexine profile and loose sexine at left margin of specimen. *c*, Delicate reticulum showing supramural ornamentation of coni and spines connected by thin longitudinal ridges (arrow). *d*, Specimen with isolated small grains (bottom arrow) on smooth nexine and areas with continuous tectum (top arrow). *e, f*, *Anacostia* pollen type. *e*, General morphology of compressed grain with short, straight sulcus and narrowing area to the left of figure. *f*, Detail of *e* showing two different kinds of lumina columellae and sculptureless muri. *a*, BTO 384. *b-d*, BTO 386. *e, f*, TH 390. Scale bars = 10  $\mu\text{m}$  (*a, b, e*), 1  $\mu\text{m}$  (*c, d, f*).

are slightly sinuous, up to 0.21  $\mu\text{m}$  thick. The muri/lumina index is 0.105. The supramural ornament varies from a smooth surface to fine transverse striations present in a few areas of the grain.

*Studied material.* Bajo Tigre BTA, BAPb MEB 366.

Anacostia Pollen Type, Friis, Crane,  
and Pedersen 1997 (Fig. 6e, 6f)

*Description.* Only one specimen of this type has been recovered from the *Ticoa harrisii* horizon at the Ticó Amphitheatre. The grain is distorted by compression and probably had a subcircular/suboval amb and a diameter of 23  $\mu\text{m}$ . The sulcus is a straight short slit that extends for half of the equatorial diameter of the grain (fig. 6e). A lateral depression extends from the straight part of the sulcus toward a narrowing area of the grain suggesting, that the aperture might be trichotomosulcate. The exine has a smooth nexine that supports a tectate-perforate to semitectate columellate and reticulate-heterobrochate sexine (fig. 6f). The columellae are up to 0.26  $\mu\text{m}$  wide and 0.32  $\mu\text{m}$  high. They are separated by distances equal to or greater than their width. The muri are up to 0.26  $\mu\text{m}$  wide, and they support a 0.32- $\mu\text{m}$ -thick tectum. The lumina are of two kinds: large, polygonal or irregular, up to 2.2  $\mu\text{m}$  wide (fig. 6f) or small, rounded (about 0.05  $\mu\text{m}$ ) that develop a tectate perforate area surrounding the sulcus (fig. 6e). Muri have a smooth surface, but occasional small granules (0.3  $\mu\text{m} \times 0.3 \mu\text{m}$ ) may be found.

### Discussion

The SEM study of palynological residues of the Anfiteatro de Ticó Formation reveals the presence of six angiospermous pollen types. The new information confirms that this group of plants was more varied during the early Aptian in Patagonia than previously suspected. The dominant genus is *Clavatipollenites*, including four species, in agreement with our present knowledge of other Aptian paleofloristic provinces (Heimhofer et al. 2007). Most *Clavatipollenites* species have been defined using LM, and it is very difficult to compare this material with specimens studied with SEM. Many authors prefer to use a neutral classification, naming the species as types or by giving them numbers. Some of the characters described here cannot be seen and measured with LM, so we decided to give numbers to the species to underscore that they were defined with SEM.

### Comparisons

*Clavatipollenites* sp. 1, 2, and 3 are the most abundant pollen taxa among angiosperms in the Anfiteatro de Ticó Formation (79 specimens studied). The three types have morphological similarities and share some characters; this is especially the case for *Clavatipollenites* sp. 1 and *Clavatipollenites* sp. 2. Intermediate forms exist (figs. 1a, 3a). However, there are minor differences in the sizes of sexine elements (lumen size slightly smaller in *Clavatipollenites* sp. 1) or in the equatorial amb, which tends to be circular in *Clavatipollenites* sp. 1 and more oval in *Clavatipollenites* sp. 2 and 3. In this respect, the indexes used (muri/lumina) have been very useful for separating the three forms, especially *Clavatipollenites* sp. 1 from *Clavatipollenites* sp. 2.

*Clavatipollenites* sp. 4, on the other hand, differs from the other *Clavatipollenites* species described here by a reticulum that has delicate sinuous muri and wide homobrochate lumina. The supermural sculpture is spiny and more pronounced than in the other species. The infratectum is clearly distinguished from the smooth and dense nexine layer. Finally, the columellae are cylindrical, not club shaped as in *Clavatipollenites* sp. 1, 2, and 3.

All four *Clavatipollenites* species show variations in the shape of the sulcus, from an almost closed linear fissure to a widely opened circular, oval, rectangular to square-shaped aperture with typical zigzag to entire margins. The sulcus membrane often shows as a sunken or collapsed area that is distinctly ornamented.

Archangelsky and Taylor (1993) described pollen found in anther masses from the Anfiteatro de Ticó Formation, Bajo Tigre locality, BTA horizon, using both SEM and TEM. The individual grains correspond closely to *Clavatipollenites* sp. 2 described here from the same plant horizon. Limarino et al. (2012, fig. 6 [26, 27]) illustrated two *Clavatipollenites* species (*Clavatipollenites* sp. 1 and 2) from the Punta del Barco Formation that closely resemble our *Clavatipollenites* sp. 3 and 2, respectively. No description and the small figures hinder further comparison.

The other two types of angiospermous pollen described here are easily differentiated from *Clavatipollenites* by a tectate-perforate exine and supramural ornamentation (smooth in the *Anacostia* type) or by a markedly heterobrochate reticulum (*Retimonocolpites* sp.). Both species are extremely rare in the Ticó pollen assemblage. Another type mentioned as Angiosperm indet. has been recently illustrated for the Ticó flora (Limarino et al. 2012, fig. 6 [25]). It shows a trichotomosulcate aperture and a columellate/microreticulate exine structure.

The beaded supramural ornament is found in many *Clavatipollenites* species. *Clavatipollenites* sp. 1 from Ticó resembles *Clavatipollenites* sp. 4 of Zavada (2003, figs. 17–19) from the lower Cenomanian of Madagascar. Shape, size, and supramural ornamentation of both species are coincident, although the shape of the sulcus is often less defined in the Patagonian species.

Heimhofer et al. (2007) illustrated pollen identified only as *Clavatipollenites* spp. and to *Clavatipollenites* cf. *hughesii* from the Cresmina Formation, late Barremian/early Aptian of Portugal. The material illustrated with LM clearly shows the gross characters of the genus (size, amb, and columellate reticulate exine), but no further details can be discerned in the excellent photographs, such as the sizes of columellae, muri, and lumina or presence of supramural ornament. *Asteropollis* sp. and *Pennipollis* sp. are also mentioned for the upper part of the Cresmina Formation (Heimhofer et al. 2007, fig. 8); these taxa are absent in the Ticó assemblage, but they are present in late Aptian strata of other units in southern Patagonia (Llorens 2003; Prámparo 1999).

Pedersen et al. (1991) described *Couperites*, a new genus of fruits found in the earliest Cenomanian (Potomac Formation) of North America. This fruit has clumps of pollen referred to *Clavatipollenites*. The grains were studied with SEM and TEM, and they show the typical exine structure as defined by Doyle et al. (1975). The thick nexine, the club-shaped columellae, and the semitectate exine including the beaded muri



were illustrated. The ultrastructure of this pollen type has been compared with members of the extant family Chloranthaceae (Walker and Walker 1984; Chlonova and Surova 1988; Pedersen et al. 1991; Friis et al. 2010a). Eklund et al. (2004), on the other hand, analyzed the phylogenetic position of *Couperites* and concluded that it is most likely related to Chloranthaceae but located below the modern clade, on the basis of its anatropous (rather than orthotropous) ovule. Therefore, *Clavatipollenites* sp. 1, 2, 3, and 4 studied here can also be reasonably related to the chloranthaceous clade.

The single specimen described here as the *Anacostia* pollen type (fig. 6e, 6f) strongly resembles *Anacostia marylandensis* pollen from the early/middle Albian of North America (Friis et al. 1997, fig. 2E–2H). This type was described as trichotomocolpate or monocolpate, with the apertures delimited by rounded ends. The exine is tectate, columellate, and reticulate, with lumina decreasing in size toward the proximal pole. Muri are not ornamented. The diameter of *A. marylandensis* pollen is 12–16  $\mu\text{m}$ , slightly smaller than the 23- $\mu\text{m}$  diameter of the Patagonian specimen. However, different sizes between mesofossil and dispersed material have been already noticed in other cases (Doyle et al. 2008). The four *Anacostia* species described by Friis et al. (1997), two from North America and two from Portugal (late Barremian to early Aptian age), show that this group was diversified by the mid-Cretaceous.

There is also some resemblance of the Patagonian *Anacostia* type pollen to *Clavatipollenites* sp. 3 (Zavada 2003, figs. 15, 16, 20, 21) from the lower Cenomanian of Madagascar. The Patagonian specimen is similar in size, shape, and smooth supramural surface. The TEM section of *Clavatipollenites* sp. 3 (Zavada 2003, figs. 20, 21) reveals a similar sexine structure, with a tectum being thicker than the height of columellae. However, in the Malagasy species, the lumina of the reticulum are not as differentiated in size as in the Patagonian specimen, although the smallest lumina also have a tendency to surround the sulcus. The aperture of the Malagasy specimen is typically monosulcate.

*Anacostia* was related to extant magnoliids (Friis et al. 1997). It most likely belongs in the near-basal order Austrobaileyales (Doyle et al. 2008). The trichotomosulcate nature of the sulcus in the Patagonian specimen strongly suggests that angiosperm plants with pollen that display this aperture type were present in the early Aptian of Patagonia (see also Limarino et al. 2012, fig. 6 [25]). The morphogenus *Similipollis* was established for dispersed pollen of this type by Góczán and Juhász (1984).

*Retimonocolpites* sp. from Ticó is somewhat similar to *Retimonocolpites* sp. 2 of Zavada (2003) from the lower Cenomanian of Madagascar. The reticulum of both species has the same disposition of small lumina adjacent to the sulcus, and the pollen wall structure is comparable, although the size and disposition of columellae are different. Furthermore, the Patagonian species differs in its smaller size (13.2  $\mu\text{m}$ ) and by the presence of scabrae on the foot layer in the Malagasy material, absent in the Patagonian specimen. *Retimonocolpites* sp. 2 is the most common species of the pollen assemblage from Madagascar (Zavada, 2003). On the contrary, only one specimen has been found in the Patagonian assemblage.

*Clavatipollenites* spp. and *Retimonocolpites* spp. have been cited and/or illustrated (mainly with LM) in other sediments

referred to the Aptian in southern South America. Most of these assemblages include other angiospermous types as well: *Asteropollis* Hedlund & Norris, *Afropollis* Doyle, Jardíné & Doerenkamp, *Retiacolpites* Schrank & Mahmoud, *Monocolpopenites* Thomson & Pflug, *Brenneripollis* Juhász & Góczán, and *Liliacidites* Couper (Archangelsky et al. 1984; Prámparo 1999; Llorens 2003; Quattrocchio et al. 2006; Vallati 2006; Medina et al. 2008; Perez Loinaze et al. 2011; Limarino et al. 2012). Some of these assemblages have been dated by ammonites and dinoflagellate cysts (Medina et al. 2008) or by radiometric methods (Corbella 2001; Césari et al. 2011). The variety of these assemblages suggests that they are slightly younger than the Ticó assemblage, and they are partly referred here to the late Aptian, in agreement with Limarino et al. (2012).

A hypothesized pattern of the early angiosperm diversification for southern South America based on fossil leaves and pollen has been recently presented (Archangelsky et al. 2009). Three stages that cover Barremian to Coniacian ages were defined. The earliest stage 1 includes fossils of Aptian age in which two levels are present. The lower level (Archangelsky et al. 2009, fig. 3) is characterized palynologically by a *Clavatipollenites* complex (1p), with the base placed at the Barremian/Aptian boundary. This complex corresponds to the Ticó flora, which we now know is more varied in angiospermous types, although *Clavatipollenites* is the dominant type. Therefore, this assemblage partly fills a gap in the chronological distribution of angiosperms and should probably be placed in the early Aptian level of stage 1, parallel to the two leaf types from the same Ticó flora: the nymphaeaphyll morphotype (Passalía et al. 2003) and a micromesophyllous, lobate, serrate leaf (Romero and Archangelsky 1986). Both types are thought to be related to basal angiosperms.

Cretaceous sediments older than the early Aptian occur in Patagonia but thus far have not yielded angiosperm leaves or pollen. This is partly the case of the Springhill Formation from some localities in Chile dated as Hauterivian (Cranwell and Srivastava 2009) or Berriasian-Valanginian in Argentina (Baldoni and Archangelsky 1983). In other localities, this unit includes slightly younger pollen assemblages (Barremian) apparently lacking angiosperms (Ottone and Aguirre Urreta 2000; Hollis et al. 2009). However, isolated records of Barremian angiosperm pollen based on borehole material was referred to the Springhill Formation (Archangelsky and Archangelsky 2004; Quattrocchio et al. 2006). The Cañadón Calcáreo Formation from Chubut province (southern Patagonia) also yielded a Late Jurassic–Hauterivian pollen assemblage without angiosperms (Volkheimer et al. 2009, fig. 1). Further research on some of these or similar units focusing on angiosperm remains are now in progress.

#### *Paleophytogeographic and Paleocological Aspects*

Brenner (1976) first recognized the southern Gondwana province, including the austral South America and South Africa as well as Australia, New Zealand, and India. South America and South Africa were at that time a paleogeographic unit (SW Gondwana of Archangelsky [2009, fig. 1]) in which at low paleolatitudes and during Berriasian–Aptian times, an equatorial (Northern Gondwana) *Dicheiropollis etruscus*/*Afropollis* palynoflora developed (Herngreen et al. 1996, fig. 3). To the

south and located at midpaleolatitudes, a transitional area included plants from the equatorial belt mixed with plants from the *Cyclusphaera psilata*-*Classopollis* subprovince (Volkheimer 1980; Vallati 2002). Tropical elements were further described for Albian rocks of the Austral Basin (Barreda and Archangelsky 2006), located at even higher paleolatitudes (greater than 60°S in Southern Patagonia).

The Ticó flora is located at the same paleolatitude as the Austral Basin. It has been studied for many years and has proven to be rich in mega-, meso- and microfossils (Del Fueyo et al. 2007). Because of the high number of endemic taxa and several species known in other regions, a paleophytogeographic unit, the Early Cretaceous Patagonian Paleofloristic Province, was suggested for this area (Vakhrameev 1988; Archangelsky 1996). This province would include the *Cyclusphaera psilata*-*Classopollis* palynological subprovince.

Angiosperm diversification in SW Gondwana occurred during the Early Cretaceous (Aptian) in coincidence with crucial geological events related to geotectonic processes that led to a breakup of Africa and South America and the gradual opening of the Atlantic Ocean (Spalletti et al. 1999). Angiosperms were rare components of plant communities in this region of Gondwana during the Aptian when compared with other plant groups (i.e., gymnosperms, pteridophytes). They mostly grew in particular environments close to lakes or rivers (Passalía et al. 2003; Friis et al. 2010a). The pollen described here was found in lacustrine to fluviodeltaic facies that suggest wet paleoenvironments during a time of strong volcanic activity (Cladera et al. 2002; Carrizo et al. 2011; Limarino et al. 2012, and references therein).

Passalía (2009) studied the atmospheric CO<sub>2</sub> content using conifer and ginkgoalean cuticles from the Anfiteatro de Ticó Formation (early Aptian) and Punta del Barco Formation (late Aptian), which represent the base and the top of the Baqueró Group, respectively. The estimated CO<sub>2</sub> content for the Ticó flora (conifer cuticles) is 700–1400 parts per million by volume. This implies a global CO<sub>2</sub> content 2.3–4.0 times higher than the present, suggesting more favorable (warm) conditions than today for the mid-Cretaceous interval in southern Patagonia.

The extension of this belt southward is possible if we take into consideration the Aptian floras found in the Antarctic Peninsula (Hernández and Ascárate 1971; Césari et al. 1999; Cantrill 2000). In many aspects, the Antarctic floras are clearly similar to the assemblages from Ticó, although the presence of Aptian angiosperms has not been reported so far. There is a reference to *Clavatipollenites* in younger strata (Albian) of the Kotick Point Formation (Dettmann and Thomson 1987), which suggests a poleward migration of the genus from Patagonia. For the moment, it is difficult to include the Antarctic assemblages in the Patagonian belt. Available paleogeographic data are not precise about the location of the Antarctic Peninsula with respect to southern Patagonia at that time, and we need further information to better evaluate possible relationships, either floristic or geographic.

## Conclusions

*Clavatipollenites* is a morphogenus of angiosperm pollen commonly found in Lower Cretaceous sediments in all paleofloristic regions. Several species have been defined with the use of LM. However, the discovery of greater diversity in exine fine structure with SEM and TEM has shown that these techniques are required for a better definition of different types (species) in *Clavatipollenites* (Chlonova and Surova 1988; Hughes 1994). The increasing importance of angiosperm distribution during this time is strengthened with the finding of six pollen types assignable to the group and described for the early Aptian Ticó flora; they belong to *Clavatipollenites* (with four types), *Retimonocolpites*, and the *Anacostia* type. *Clavatipollenites* clearly dominates angiosperm pollen assemblages in the same horizons where angiosperm leaf remains have also been described. Pre-Aptian angiosperms may have been present in Patagonia, as suggested by isolated records of *Clavatipollenites* in the Springhill Formation (Archangelsky and Archangelsky 2004; Quattrocchio et al. 2006). At present, the angiosperms found in the Ticó flora stand as the oldest Aptian record of the group in southern South America and in SW Gondwana.

The paleoenvironment in which the angiosperm pollen was found indicates wet and humid conditions (Cladera et al. 2002; Limarino et al. 2012), while paleoclimatic data based on cuticular studies report a high CO<sub>2</sub> atmospheric content and warmer global temperatures (Passalía 2009). These data agree with the ecological requirements of the Chloranthaceae, a group of basal angiosperms to which *Clavatipollenites* is related.

*Clavatipollenites* is found at a high paleolatitude (greater than 60°S) as a member of rich plant communities that were recurrently disturbed by strong volcanic activity. The humid, wet, and warm conditions found in the Ticó area probably favored the development of basal angiosperms preventing or diminishing the damage caused by fire and heavy ash fall.

Finally, Patagonia is becoming a fruitful Gondwana area for palynological and paleobotanical research of Early Cretaceous angiosperms considering the presence of pre-Aptian, Aptian, and Albian formations with well-preserved materials that can be studied with both SEM and TEM.

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