

Early Cretaceous palm pollen tetrads from Patagonia, Argentina



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ABSTRACT

Pollen tetrads and monads of spiny pollen grains with close affinities to palms have been found in several localities from the Lower Cretaceous (Barremian–Albian) of the Austral Basin (Magallanes), Patagonia (Argentina). When found dispersed, spiny and zonosulcate pollen grains, are commonly referred to the fossil genus *Spinizonocolpites* Muller, with close affinities to the extant palm *Nypa*. The Patagonian specimens were compared with fossil and extant members of the Arecaceae, showing close similarities in shape and sculpture with the primitive members of the subfamily Calamoideae. *Nypa* produces tetragonal tetrads different from the tetrahedral tetrads of the *Spinizonocolpites*-type recovered from Patagonia. The specimens were studied with LM and SEM. The polarity, aperture orientation and tetrad type allow segregating the Patagonian grains from the Nypoideae and relating it to the Calamoideae subfamily. These records suggest an antique origin of monocots and a probably initial diversification of calamoid palms during the Early Cretaceous in high latitudes of Gondwana. The presence of palmas during the Early Cretaceous in southern South America suggests a warm and humid climate, similar to that found in present days at tropics.

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1. Introduction

The Patagonian Early Cretaceous palynofloras are known to be varied in their spores and pollen content (Del Fueyo et al., 2007; Archangelsky et al., 2009). Lycophyte and Bryophyte spores, as well as gymnospermous pollen (mostly from conifers), are well represented. Other taxa are subordinate: ginkgophytes, seed ferns, and primitive magnoliophytes. Recent palynological research of Patagonian Lower Cretaceous strata suggests that magnoliophyte pollen was more diverse than previously suspected (Poire et al., 2002; Llorens, 2003; Archangelsky and Archangelsky, 2004; Quatrocchio et al., 2006; Vallati, 2006; Medina et al., 2008; Pérez Loinaze et al., 2013). In the present study, we describe magnoliophyte pollen grains found at three localities in the Austral Basin (Patagonia, Argentina). The spiny pollen grains, which occur mainly as tetrads, show several features that are typical of monocots, and particularly to primitive members of palms. The data presented

here are significant because they suggest an early diversification of monocots and related plants (e.g. palms) back in the Barremian/Albian, at least in South America.

Pollen grains related to palms have also been found in the Albian and Cenomanian of Africa (Schrank and Awad, 1990). However, *Spinizonocolpites* represents the earliest undisputed palm pollen (Harley, 2006 and references therein). Whereas the oldest macrofossil record of palms is from the upper Coniacian – lower Santonian of U.S.A., and the lower Campanian of Austria (Kvaček and Herman, 2004; Pan et al., 2006).

In Patagonia Argentina, the oldest palm macrofossils occurred in the Upper Cretaceous of the Neuquén Basin (Andreis et al., 1991; Ancibor, 1995; Martínez, 2013). Therefore, the finding of Early Cretaceous palm pollen in the Austral Basin opens a new perspective to elucidate their early evolution in SW Gondwana.

2. Geological setting

The fossil material described herein was recovered from three different localities along the Austral Basin: Cerro Bayo (Piedra Clavada and Kachaike Formations), Bajo de la Comisión (Río Mayer and Kachaike Formations) and the Shell MLD 3 well in the

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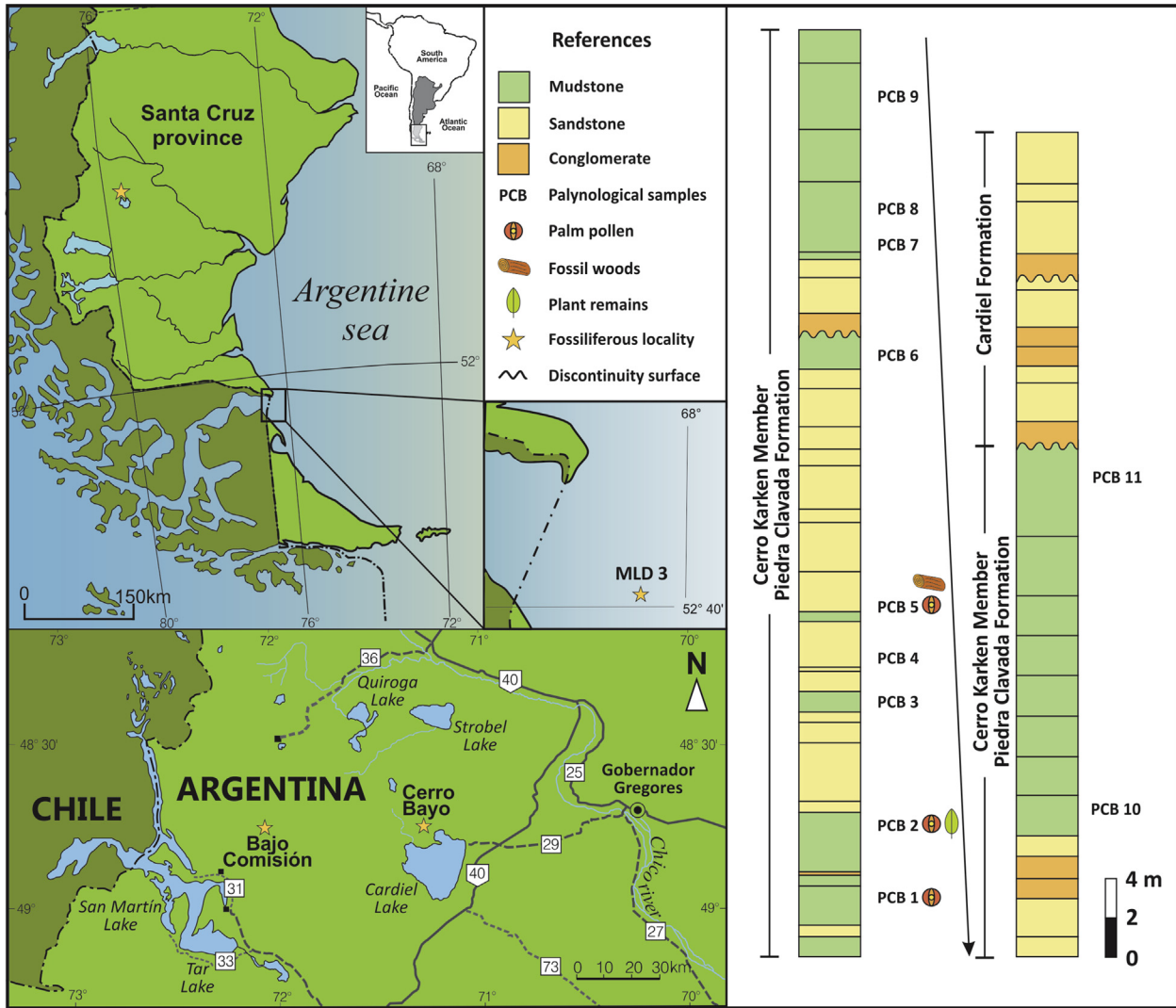


Fig. 1. Location map of the fossiliferous localities and sedimentological log of Cerro Bayo locality.

Argentine offshore Platform (probably Springhill Formation) (Fig. 1).

The Cerro Bayo locality is placed North of Cardiel Lake in Santa Cruz province (Patagonia, Argentina) (Fig. 1). The Cerro Bayo

section (PCB) yielded relatively abundant palynomorphs found in the Piedra Clavada Formation, Cerro Karken Member (Ramos, 1982). Ammonites are known to occur in this member in equivalent beds at Querol and Río Cardiel sections (Ramos, 1982):



Fig. 2. Cerro Bayo locality. 1. General view of Piedra Clavada Formation of Cerro Bayo locality (Santa Cruz province, Argentina).

presence of the genera *Beudanticeras* and especially the *Cleoniceras* subgenus *Neosaynella cardielense* Leanza suggest an early Albian age to Piedra Clavada Formation (Casey, 1954).

The pollen grains have been identified in all six fossiliferous levels of the Cerro Bayo section (Fig. 1), although it is more frequent at the levels PCB 1 and PCB 5 (Guler et al., 2015). Sporomorph assemblages are dominated by bryophyte-pteridophyte spores and pollen grains of conifers (mainly *Classopollis* and araucariaceous pollen). Partly redeposited marine microplankton has been found only at the uppermost PCB 11 fossiliferous level.

At the Bajo de la Comisión section (PBC, see Fig. 2 in Archangelsky et al., 2012), few grains with palm affinity have been found in the basal units 2–3 and 4–6. Prodelta and delta front facies that belong to the uppermost beds of the Río Mayer Formation, in transition to the Kachaike Formation yielded marine dinoflagellates that were referred to the Australian *Muderongia tetracantha* interval zone of an early Albian age (Guler and Archangelsky, 2006). Pollen grains of *Arecipites* are also commonly found at the same levels (see fig. 6FO in Archangelsky et al., 2012).

The Piedra Clavada and Kachaike formations are units of a subcycle of the Lago San Martín sedimentary cycle (see fig. 4 in Arbe, 2002). Both were deposited during the continentalization of the Austral Basin when a slow southward sea regression occurred during the Aptian–Albian. Variable sedimentary restricted marine deposits (platform, delta front, playa, etc.) are found as slightly heterochronous units. *Spinizonocolpites* pollen type occasionally occurs in both formations.

The offshore borehole Shell MLD 3, located on the Argentine Continental Platform facing the Santa Cruz province has also yielded *Spinizonocolpites* type grains at the base of the section (1579 m and 1564 m, Archangelsky and Archangelsky, 2004), where a shallow marine sedimentation begins (Springhill Formation). The dinoflagellates cysts found in the same beds correspond to the Australian *Muderongia tetracantha* zone of late Barremian age (Guler et al., 2015). Other palm pollen grains corresponding to the genus *Arecipites* were also recovered from the same beds (see figs. 6G and 6I in Guler et al., 2015).

The Piedra Clavada Formation lays conformably over the uppermost sediments of the Río Mayer Formation, which was dated with ammonites as late Aptian (Medina et al., 2008). It is essentially of a deltaic origin with different types of facies (prodelta, deltaic front, interdistributary channels and shoreface-playa) in which the participation of well-preserved plant debris and fossil wood are common, suggesting little transport from some close terrestrial deposits (Poire et al., 2002).

3. Materials and methods

Most of the samples studied here were collected in 2001 by one of the authors (S.A.) from six levels of a section 90 m thick of the PCB Cerro Bayo section (Fig. 2). Few other specimens were recovered from the PBC Bajo Comisión section and the borehole Shell MLD-3 (1584.01 m deep) (Fig. 1).

All slides are stored in the Palynological Section of the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (BA Pal). The sediments were processed with HCl and HF to eliminate carbonates and silicates respectively, then subjected to sieving with 10 μm , 25 μm and 200 μm meshes polyester sieves and the residue was mounted in glycerine-jelly following the technique of Gamarro and Cárdenas (1980).

The original rock specimens and the residues are stored in the “División Paleobotánica” of the same Museum. Microscopes Zeiss Axioscope 2 and Leitz Diaplan were used for observation while digital cameras Coolpix 995 and Leica 280 were used for

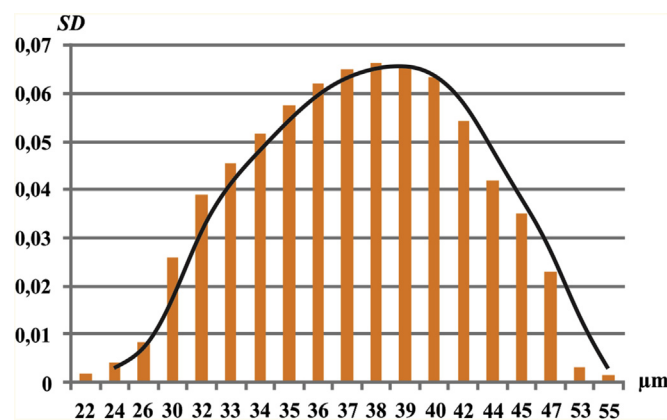


Fig. 3. Gaussian distribution based on the dimensions of *Spinizonocolpites*-type pollen grains (SD: Standard deviation), based on specimens from Cerro Bayo, Bajo Comisión and MLD 3 localities.

photography. We processed the images using the software CombineZP (Hadley, 2006).

In addition, the Scanning Electron Microscope (SEM) of the Museo Argentino de Ciencias Naturales (MACN), Phillips XL 30 TMP was used for observation and photography. The corresponding stubs are housed in the “División Paleobotánica” with the acronym BAPb MEB.

Sixty-three pollen grains were counted, and measured in nine slides. The pollen size shows a Gaussian distribution; furthermore, we used these data to calculate the maximum, minimum, and arithmetic mean, mode and standard deviation values (Fig. 3). For the morphological description of the material, we used the terminology proposed by Punt et al. (2007).

Slides and MEB stub

Cerro Bayo locality: PCB 1 (BA Pal 5668, 5697, 6325 and BA Pb MEB 524). PCB 2 (BA Pal 6326, 6328). PCB 5 (BA Pal 6327).

Bajo Comisión locality: PBC 11 (BA Pal 6329). PBC 15 (BA Pal 6330).

Offshore: SHELL MLD-3 (BA Pal 6292).

Localities and stratigraphic horizon

Cerro Bayo (Piedra Clavada Formation – “Karken member”). Lower Cretaceous (Albian). Santa Cruz province, Argentina.

Bajo Comisión (Kachaike Formation). Lower Cretaceous (Albian), Santa Cruz province, Argentina.

MLD 3. Offshore (Springhill Formation). Lower Cretaceous (Barremian), Argentina.

4. Description of the material and comparisons

All the analysed samples contain both tetrads and/or monads of zonalsulcate spinous pollen grains considered here preliminarily as part of the *Spinizonocolpites*-type.

The tetrads are tetrahedral and contain four identical grains (Fig. 4). The tetrad has a mean diameter of 56.1 μm (38–67.5). The single grains are oval to elliptic and flattened along the polar axis, generally separated by an equatorial aperture (incomplete zonalsulcus) which divides the grain into two, more or less, equal parts (Figs. 4.1–4.3). In the tetrad, the grains have an average polar diameter of 31.31 μm and an equatorial diameter of 44.61 μm .

The single grains have a mean diameter of 38.2 μm (22–55) (Fig. 5). The exine is 3 μm thick, tectate, perforate, bearing numerous and scattered suprategate solid and conspicuous spines (Figs. 5.4–5.6). The grains have a microreticulate exine,

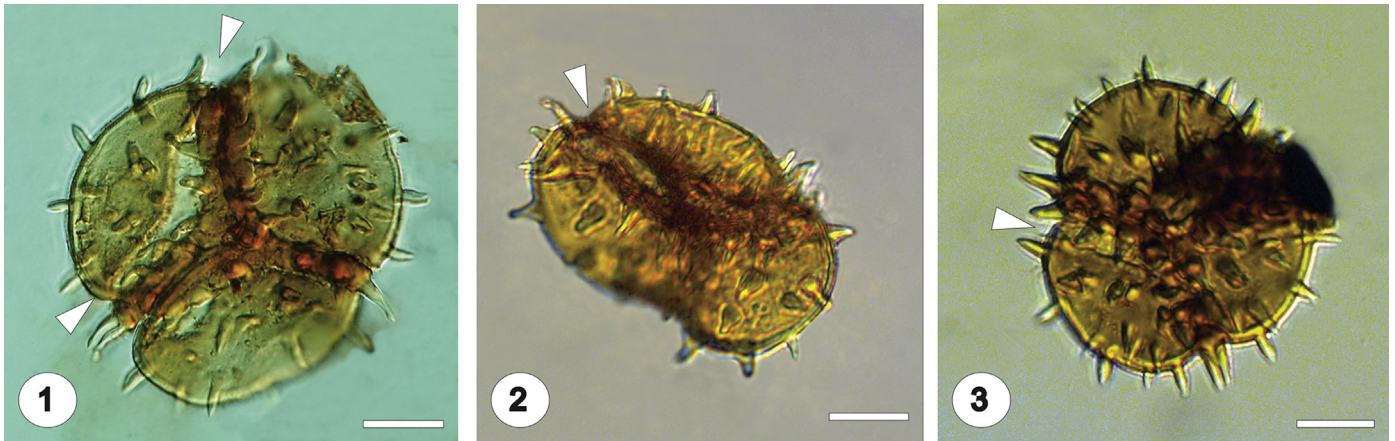


Fig. 4. *Spinizonocolpites*-type. Tetrads. All light microscope (LM). All scales = 15 µm. 1. Tetrahedral tetrad showing sulcus and supratectal spines. Zonosulcus (white arrows), BA Pal 5697.2-3. Tetrahedral tetrad. Zonosulcus (white arrows). 2. BA Pal 6327. 3. BA Pal 6325.

the fine reticulum shows as minute circles (black-white with LO analysis).

The spines are uniformly spaced, conical to subconical, with an expanded base and pointed apex, straight to slightly curve. Their basal diameter reaches 1.8 µm, and the length varies among 5–10 µm. Surface between the spines irregularly perforate (observed in SEM images from Fig. 6).

Echimonocolpites tersus Ward (1986) from the upper Albian of Kansas (USA) and *Echimonocolpites* cf. *E. tersus* from the Albian of Sudan (Schrank, 2001) have smooth and dense wall in the spaces between the spines and a monosulcate aperture, whereas *Spinizonocolpites*-type grains from Patagonia (Argentina) are zonosulcate with microreticulate exine.

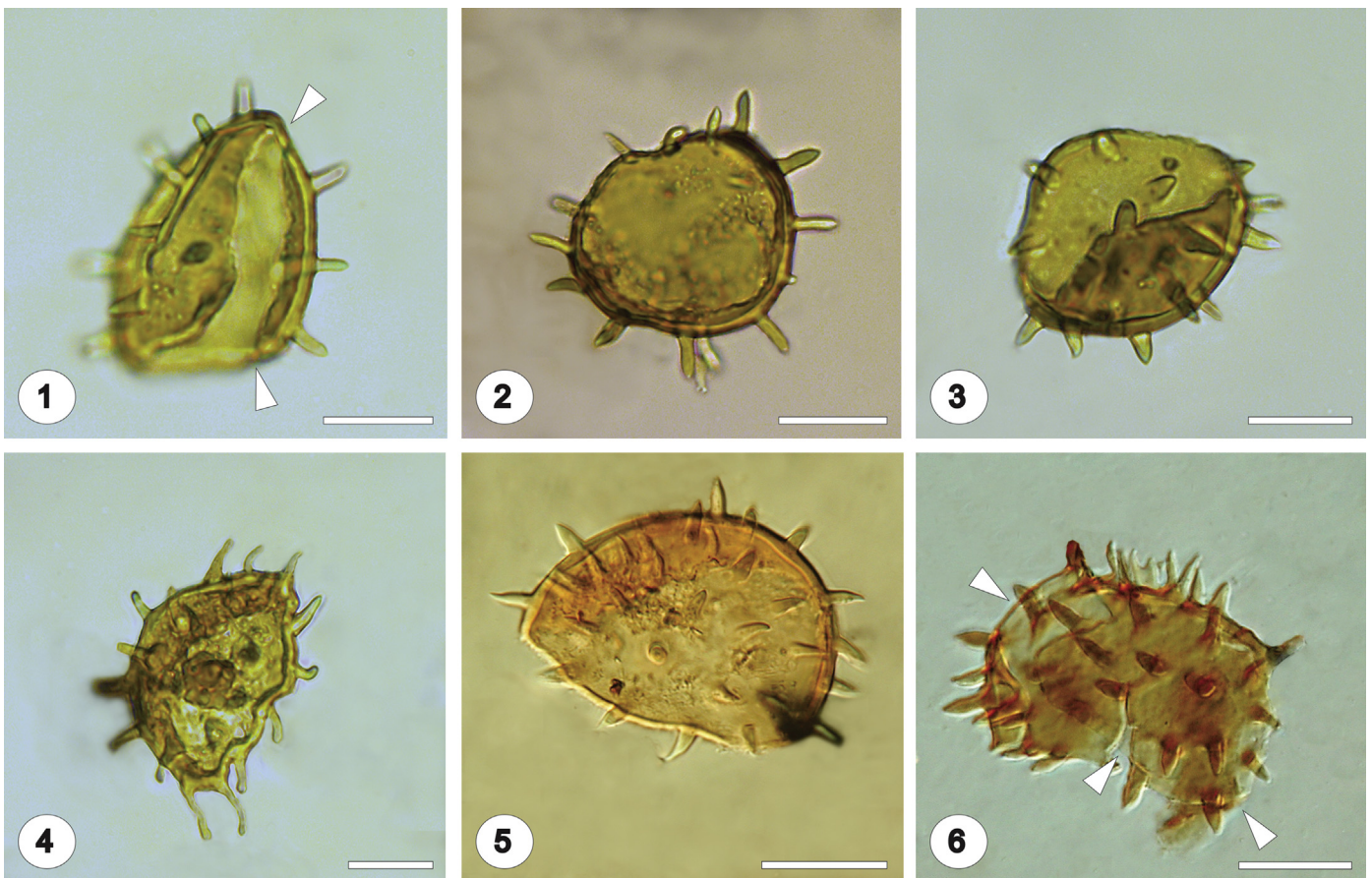


Fig. 5. *Spinizonocolpites*-type. Monads. All LM. All scales = 15 µm. 1-6. Monads showing spines and zonosulcus (white arrows). 1. BA Pal 6325. 2. BA Pal 6326. 3. BA Pal 6325. 4. BA Pal 6325. 5. BA Pal 5668. 6. Broken specimen showing spines and zonosulcus (white arrows), BA Pal 6292.

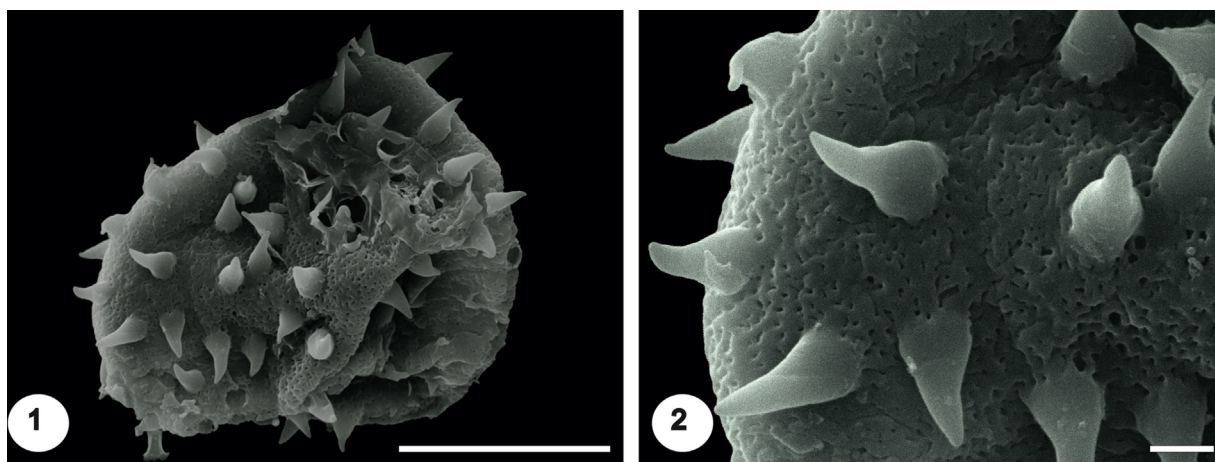


Fig. 6. *Spinizonocolpites*-type. Monad. All SEM. 1–2. BA Pb MEB 524. Monad. Scale = 10 μm . 2. Detail of perforate sculpture. Scale = 1 μm .

5. Botanical affinity of the pollen tetrads

Among fossil taxa, spiny tetrahedral tetrad pollen grains characterized the genus *Droseridites* Cookson ex Potonié (1960); however, this genus has inaperturate grains.

The pollen grains referred to the genus *Spinizonocolpites* Muller (1968), are usually considered to represent palm pollen (Germeraad et al., 1968; Zetter et al., 2001).

The Palmae family possesses pollen grains with varied aperture number (Sowunmi, 1972), orientation and exine ornamentation, a combination of characters that are present in the fossil pollen described here. Harley and Baker (2001) classified the pollen grains of extant palms in 17 aperture types, two of which, viz. “incomplete zonosulcate” and “zonasulcate” types are present in our fossils. These types are known in three subfamilies: Arecoideae, Calamoideae and Nyipoideae. The last two possess spines in the exine, but the Nyipoideae have tetragonal tetrads (Harley and Baker, 2001) (Table 1). Therefore, we confine our analysis to the subfamily Calamoideae that has tetrahedral tetrads, spiny grains with an equatorial and zonate aperture.

Different taxa of fossil pollen are related to palms, although those referred to the genus *Spinizonocolpites* Muller (1968) resemble more to our material because it is the only one with a zonosulcus and a spiny surface. Several authors compare *Spinizonocolpites* with the pollen of the recent genus *Nypa* (Muller, 1968; Singh, 1999; Harley and Baker, 2001; among others). Because the fossil *Spinizonocolpites* grains are related with extant monotypic genus *Nypa*, both genera should also share similar microsporogenesis type, polarity and size. However, *Nypa* has a tetragonal state of the tetrad and pollen grains with a size between 45 and 70 μm (Kedves, 1980; Harley et al., 1991); and conversely, the Patagonian grains have a tetrahedral tetrad, and are smaller (22 μm –55 μm) than *Nypa*.

However, it is interesting to mention that *Spinizonocolpites* encompasses species with a great variability of pollen size. The type species of *Spinizonocolpites* (*S. echinatus* Muller) has small dimensions, with a size of 33–43 μm (Muller, 1968). In contrast, *Spinizonocolpites baculatus* Muller and other species of *Spinizonocolpites* have sizes closer to the extant *Nypa* with size up to 76 μm (Tables 1 and 2).

The subfamily Calamoideae has tetrahedral tetrads and spiny grains with an equatorial and zonate aperture. This subfamily has mainly equatorial disulcate pollen; however, there are species with an incomplete zonosulcate aperture in the genera *Daemonorops* Blume, *Korthalsia* Blume and *Salacca* Reinwardt (Sowunmi, 1968; Dransfield, 1980; Dransfield et al., 1990). *Daemonorops* has diporate grains with spines while the pollen of *Korthalsia* is zonosulcate but has a gemmate exine and shows some similarity to *Paravuripollis* Rao et Ramanujam. On the other hand, the pollen of some species of the modern genus *Salacca* is spiny and has an ultrastructure similar to *Nypa* Steck. However, the pollen grains of *Salacca* are commonly much smaller (less than 30 μm) than those of *Nypa* (Ferguson, 1986; Harley and Baker, 2001).

The peculiar tetrads of the Patagonia assigned to the *Spinizonocolpites*-type are unequivocally referred to the palm subfamily Calamoideae. The main characters that this subfamily shares with our material are: tetrahedral tetrad, spiny grains with equatorial and zonate aperture and small pollen grains (less than 55 μm in diameter).

We here underscore the tetrahedral state of the tetrad, which suggests a simultaneous microsporogenesis type and polarity of the pollen among monocots: only three families possess this type: Areaceae, Araceae and Rapataceae (Furness and Rudall, 1999). In our case, the presence of a tetrad allows to infer the polarity and aperture orientation and therefore segregate our grains from the Nyipoideae and relate it rather to the Calamoideae subfamily.

Table 1

Comparison among *Spinizonocolpites*-type and some extant zonosulcate pollen grains of Nyipoideae and Calamoideae (Palmae).

	Geographical area	Exine	Dimensions (μm)		References
<i>Spinizonocolpites</i>-type	South America – Patagonia	Tectate, perforate, microreticulate, with suprategal spines	22	55	This paper
<i>Nypa fruticans</i> Wurm	Estuarine habitats of the Indian and Pacific Oceans	Tectate, densely perforate with suprategal spines	45	70	Harley et al., 1991; Kedves, 1980.
<i>Salacca secunda</i> Griff.	Indonesia and Malaysia	Tectate smooth, sparsely perforate or foveolate	19	27	Ferguson, 1986.
<i>Salacca clemensiana</i> Becc.	Phillipines and northern Borneo	Tectate, densely perforate, with suprategal spines	18	26	Ferguson, 1986.
<i>Korthalsia</i> spp.	Indo-China to New Guinea	Intectate, gemmate, clavate, spinose and spinulose or scabrate	21	45	Ferguson, 1986.

Table 2
Comparison among *Spinizonocolpites* species.

	Geographical area	Stage	Dimensions (µm)	Features
<i>Spinizonocolpites</i>-type (this paper)	Patagonia – South America	Lower Cretaceous	22–55	Exine: 3 µm. Length spines: 6.4 µm. Diameter spines: 1.8 µm.
<i>Spinizonocolpites baculatus</i> Muller (1968)	Malaysia – Asia	Cretaceous-Eocene	37–62	Exine: 1–2 µm. Bacula: 7–13 µm long.
<i>Spinizonocolpites adamanteus</i> Frederiksen (1994)	Pakistan – Asia	middle to upper Paleocene	46–76	Exine: 2–3.5 µm. Length spines: 6–10 µm. Diameter spines: 3–8 µm. Spines rounded diamond shaped in side view.
<i>Spinizonocolpites breviechinatus</i> Jaramillo et Dilcher (2001)	Central Colombia – South America	middle Paleogene	40–65	Exine: 1 µm. Length spines: 2–4 µm. Diameter spines: 1–2 µm.
<i>Spinizonocolpites bulbospinosus</i> Singh = <i>S. kutchensis</i> (Venkatachala et Kar) Frederiksen Singh (1990)	Northeastern India	Paleocene	33–63	Exine: 1–1.5 µm. Length spines: 3.5–6 µm. Diameter spines: 2–5 µm.
<i>Spinizonocolpites</i> -complex Scafati, Melendi, and Volkheimer (2009)	San Jorge Basin, Patagonia – South America	Paleogene	40–50	Exine: tectate, perforate to microreticulate. Spines: Thin, low conical, rounded conical or verrucate and baculae also bulbous at the base.
<i>Spinizonocolpites echinatus</i> Muller (1968)	Malaysia	Cretaceous – Eocene	33–43	Exine: 2 µm. Length spines: 5–7 µm. Spines slightly expanded base, conical echinae.
<i>Spinizonocolpites grandis</i> Jaramillo et Dilcher (2001)	Central Colombia – South America	middle Paleogene	70–85	Exine: 0.5–1 µm. Length spines: 4–5 µm. Diameter spines: 3–4 µm.
<i>Spinizonocolpites hialinus</i> Archangelsky et Zamaloea (1986)	Patagonia – South America	Paleocene	33–55	Exine: 1.5 µm, hyaline. Length spines: 5 µm.
<i>Spinizonocolpites indicus</i> Singh (1990) (= <i>S. echinatus</i> = <i>S. prominatus</i> according to Frederiksen 1994)	Northeastern of India	upper Paleocene	41–58	Exine: 1–1.5 µm. Length spines: 7–15 µm. Diameter spines: 2–4 µm.
<i>Spinizonocolpites intrarugulatus</i> Muller, Di Giacomo et Van Erve (1987)	Western Venezuela – South America	Maastrichtian	34–42	Exine: 2.5–3 µm. Bacula: up to 10 µm, expanded bases, sometimes bifurcate, collumellae fused into an intrarugulate pattern.
<i>Spinizonocolpites pachyexinatus</i> Jaramillo et Dilcher (2001)	Central Colombia – South America	middle Paleogene	70–80	Exine: 3–5 µm. Length spines: 7–10 µm. Diameter spines: 5–6 µm.
<i>Spinizonocolpites perspinosus</i> (Couper) Hekel (1972)	Queensland, Australia	Pliocene	25–44	Exine: 1–1.5 µm. Length spines: 4–6 µm Diameter spines: 2 µm.
<i>Sinizonocolpites prominatus</i> (McIntyre) Stover et Evans (1973) ^a	offshore Gippsland Basin, Australia	lower and middle Eocene	?	Length spines: 4–9 µm. Long conical spines, commonly bulbous at the base.
<i>Spinizonocolpites pengchiahsuensis</i> Shaw (2000)	Taiwan – Asia	Eocene	35–47	Exine: 1 µm Reticulate
<i>Spinizonocolpites</i> sp A Singh (1990)	Northeastern of India	Paleocene	60–92	Exine: 1–2 µm. Length spines: 3–10 µm. Diameter spines: 2–5 µm.
<i>Spinizonocolpites spinulosus</i> Ramanujam (1987)	South of India	Neogene	14–28	Exine: 1.8 µm. Microreticulate.
<i>Spinizonocolpites wodehousei</i> Singh (1990) (= <i>S. baculatus</i> according to Frederiksen 1994)	Northeastern of India	Paleocene	34–65	Exine: 1–1.5 µm. Length spines: 8–18 µm. Diameter spines: 4–7 µm.

^a Intermediate in morphology between *S. baculatus* and *S. echinatus* according to Schrank (1994); Stover et Evans considered *S. prominatus* = *S. echinatus*.

6. Discussion

6.1. Systematics and ecology of palms

At present, the family Arecaceae Schultz-Schultzenstein 1832, *nom. conserv.* or Palmae Jussieu, *nom. cons. et nom. alt.* (palms) consists of perennial plants with a great variety of morphology (trees, large rhizomatous herbs, or lianas). The palms have 190 genera with 2000 species, distributed across warm climates of the world, being important and typical plants of tropical sites (Dransfield and Uhl, 1998; Simpson, 2006).

Palms are excellent indicators of palaeoclimatic conditions, because they are a typical family with a subtropical and tropical distribution, and they commonly grow in areas where the mean annual temperature is higher than 10 °C, with mean temperatures

in the coldest month being more than 5 °C (Greenwood and Wing, 1995; Harley, 2006).

The Arecaceae are a monophyletic group, but the classification of palm sub-families presents numerous ambiguities. For this reason, we follow here the work of Asmussen et al. (2006) based on molecular data and morphological characters. They divided the palms into 5 sub-families: Calamoideae, Nypoideae, Coryphoideae, Ceroxyloideae and Arecoidae.

6.2. Ancestry, phylogeny and records of palms

In flowering plant evolution, it is accepted that monocots diverged very early from other magnoliophytes; however, palaeobotanical evidence of monocots from the earliest phases of flowering plants are scant (Crepet et al., 2004; Friis et al., 2010; Magallón et al., 2013).

The pollen grains of living monocots are either monocolpate or trichotomocolpate, and may be difficult to distinguish from the pollen of some basal angiosperms (ANITA-grade, Chlorantaceae and eumagnoliids) (Harley and Baker, 2001; Harley and Dransfield, 2003). This situation is identical to Cretaceous angiosperm pollen grains, because the morphological and structural features that potentially distinguish monocots pollen from basal angiosperms pollen are relatively subtle (Friis et al., 2010).

An early record of the monocot pollen assigned to Pothoideae-Monstereae has been dated in the late Barremian – early Aptian of Portugal (Friis et al., 2004). Nevertheless, the identity of some of these grains has been questioned (Hoffmann and Zetter, 2010). However, macrofossils with close affinities to Araceae (Aroideae) have been discovered in deposits of the upper Barremian – Aptian in Portugal (Friis et al., 2010).

On the other hand, it is interesting to notice that the fossil pollen here studied is nested inside the monocots, and especially in the palms. These records of pollen grains with palm affinity in the late Barremian-Albian agree with molecular data on the origin of monocots and palms during the Early Cretaceous.

The palms probably appeared in the Early Cretaceous according to phylogenetic studies that date the stem group of Arecaceae ca. 120 Ma (Albian) and a divergence within the crown group to ca. 110 Ma (Janssen and Bremer, 2004). The Patagonian material pushes down the oldest record of palms to a late Barremian-early Aptian age, according to data based on marine dinoflagellates (Guler et al., 2015).

Furthermore, the monocot pollen record in Lower Cretaceous strata forces us to pay attention to the origin and antiquity of monocots in relation to the early magnoliophyte lineages (Amborelales, Nymphaeales, Austrobaileyales and “magnoliids”) (Doyle et al., 2010). Therefore, this fossil evidence suggests that monocots and eudicots were present early in the late Mesozoic, as suggested by Burger (2012).

Macrofossil records of palms are known from the Aptian of Egypt (Vaudois-Miéja and Lejal-Nicol, 1987) and the Turonian of France (Crié, 1892). However, the earliest unequivocal fossil occurrences are from the upper mid-Cretaceous to the lower Upper Cretaceous, and they consist of leaves named *Sabalites* Saporta, from the upper Coniacian – lower Santonian of U.S.A. (Berry, 1914), and the lower Campanian of Austria (Kvaček and Herman, 2004).

Most authors agree that *Spinizonocolpites* may represent the earliest undisputed palm pollen, with records in the Maastrichtian, together with other Maastrichtian palm-like pollen taxa such as *Mauritiidites* and *Longapertites* as well (Schrank, 1994; Harley,

2006). Therefore, our findings of *Spinizonocolpites*-type tetrads in the upper Barremian of Patagonia extends back in time the oldest known records of palm pollen in Gondwana.

6.3. Argentine records

The fossil records of palms in Argentina consist of pollen grains, seeds and stems.

One of the most common fossils of Arecaceae is *Palmoxylon* Schenk with 10 species from the Cretaceous to the Neogene. *Palmoxylon garridoi* Martínez (2013) from the Campanian of the Anacleto Formation (Neuquén Basin) in Patagonia, is the earliest stem of palm found in Argentina, assigned to the extant subfamily Calamoideae. Other stems that come from Maastrichtian to Neogene are listed in Table 3.

Palm seeds have been found in Cretaceous strata of Northern Patagonia (Allen Formation); based on the endosperm morphology affinities with the extant *Phoenix* are suggested (Andreis et al., 1991; Ancibor, 1995). Finally, Futey et al. (2012) described fossil fruits of palms from the Salamanca Formation (Paleocene, Danian) in Chubut province (Patagonia), with affinities to the Arecaceae subfamily.

The pollen records of palms in Argentina are numerous and diverse, from the Cretaceous to the Miocene, represented by several genera: *Arecipites* Wodehouse, *Confertisulcites* Anderson, *Longapertites* van Hoeken-Klinkenberg, *Monogemmites* Krutzsch, *Monosulcites* Cookson ex R. A. Couper, *Pandaniidites* Elsik, *Proxapertites* van der Hammen, *Sabalpollenites* Thiergart ex Raatz and *Spinizonocolpites* Muller. The details of species, their provenance and references are listed in Table 4.

6.4. Biogeographical, palaeoecological and biostratigraphical significance

The pollen tetrads studied here, and their affinities with some taxa of Calamoids suggest that some palaeoecological conditions (e.g. warm and humid climate) prevailed during the Early Cretaceous in the Austral Basin.

The *Spinizonocolpites* type tetrads here described are related to the extant genus *Salacca* (Calamoideae). The Calamoideae subfamily is one of the best defined, and morphologically the most diverse in the palm family (Baker et al., 2000). They are distributed throughout the wet tropical regions of the world (Asia, America and Africa), but are particularly well represented in west Malaysia (Baker et al., 2000). They comprise 22 genera and approximately

Table 3
Argentine records of *Palmoxylon* Schenk.

	Stage	Formation	References
Neuquén Basin			
<i>Palmoxylon garridoi</i>	Upper Cretaceous (Campanian)	Anacleto	Martínez (2013)
<i>Palmoxylon santarosense</i>	Upper Cretaceous (Maastrichtian)	Allen	Ancibor (1995)
<i>Palmoxylon rionegrense</i>	Upper Cretaceous (Maastrichtian)	Allen	Ancibor (1995)
<i>Palmoxylon valchetense</i>	Upper Cretaceous (Maastrichtian)	Allen	Ancibor (1995)
<i>Palmoxylon pichaihuensis</i>	Upper Cretaceous-Paleogene	“Colipilli Group”	Ottone (2007)
San Jorge Basin			
<i>Palmoxylon patagonicum</i>	Paleogene (Danian)	Bororó	Romero (1968)
<i>Palmoxylon bororensis</i>	Paleogene (Danian)	Bororó	Arguijo (1978)
<i>Palmoxylon varetum</i>	Paleogene (Danian)	Bororó	Arguijo (1981)
<i>Palmoxylon sp 1</i>	Paleogene (Danian)	Bororó	Petriella (1972)
<i>Palmoxylon sp 2</i>	Paleogene (Danian)	Bororó	Petriella (1972)
Santa María Basin			
<i>Palmoxylon romeroi</i>	Neogene (Upper Miocene)	Chiquimil	Franco et al. (2014)
Paraná Basin			
<i>Palmoxylon concordiense</i>	Neogene (Pliocene)	Ituzaingó	Lutz (1980, 1986)
<i>Palmoxylon yuqueriense</i>	Neogene (Pliocene)	Ituzaingó	Lutz (1984), Franco (2014)

Table 4
Argentine records of palm pollen.

	Stage	Formation	References
Austral Basin			
<i>Spinizonocolpites</i> -type	Lower Cretaceous (Barremian)	Springhill	This paper
	Lower Cretaceous (Albian)	Piedra Clavada, Kachaika	This paper
<i>Arecipites</i> sp.	Lower Cretaceous (Albian)	Kachaika, Punta del Barco	Archangelsky et al. (2012)
<i>Proxapertites</i> sp.?	Lower Cretaceous (Albian)	Kachaika	Archangelsky et al. (2012)
<i>Spinizonocolpites</i> -Type	Lower Cretaceous (Albian)	Kachaika	Archangelsky et al. (2012)
<i>Arecipites minutiscabratus</i> McIntyre 1968	Upper Cretaceous (Maastrichtian)	La Irene	Povilauskas et al. (2008)
<i>Arecipites</i> sp.	Upper Cretaceous (Maastrichtian)	La Irene	Povilauskas et al. (2008)
<i>Longapertites</i> sp.	Upper Cretaceous (Maastrichtian)	La Irene	Povilauskas et al. (2008)
<i>Spinizonocolpites hialinus</i> Archangelsky et Zamaloa, 1986	Upper Cretaceous (Maastrichtian)	La Irene	Povilauskas et al. (2008)
<i>Arecipites minutiscabratus</i> (McIntyre, 1968) Milne	Upper Cretaceous (Maastrichtian)	Monte Chico	Povilauskas (2013)
<i>Spinizonocolpites hialinus</i> Archangelsky et Zamaloa	Upper Cretaceous (Maastrichtian)	Monte Chico	Povilauskas (2013)
<i>Spinizonocolpites</i> sp.	Upper Cretaceous (Maastrichtian)	Monte Chico	Povilauskas (2013)
<i>Proxapertites operculatus</i> (Ham.)Hammen	Paleocene	Salamanca	Barreda (2002)
<i>Arecipites</i> cf. <i>A. minutiscabratus</i> McIntyre	Oligocene	San Julián	Barreda (1997)
<i>Arecipites subverrucatus</i> (Pocock.) Mild. et Pock.	Oligocene – Miocene	Monte León	Barreda (2002)
Neuquén Basin			
<i>Spinizonocolpites</i> sp.	Upper Cretaceous (Maastrichtian?)	Loncoche	Papú (2002)
<i>Spinizonocolpites</i> sp.?	Upper Cretaceous (Maastrichtian)	Allen	Vallati (2010)
Golfo de San Jorge Basin			
<i>Confertisulcites</i> sp.1	Palaeogene	Salamanca and Bororó	Archangelsky, (1973)
<i>Confertisulcites</i> sp.2	Paaleogene	Bororó	Archangelsky, (1973)
<i>Longapertites andresii</i> Archangelsky	Paaleogene	Bororó	Archangelsky, (1973), Volkheimer et al., (2007)
<i>Longapertites patagonicus</i>	Cretaceous -Palaeogene	Lefipan, Salamanca and Bororo	Archangelsky, (1973), Baldoni & Askin, (1993), Volkheimer et al., (2007)
<i>Longapertites</i> sp.	Palaeocene	Salamanca	Archangelsky, (1973)
<i>Monogemmmites gemmatus</i> (Couper) Krutzsch 1970 emend. Mildenhall	Palaeocene	Bororó	Volkheimer et al., (2007)
<i>Monosulcites minutiscabratus</i> McIntyre	Cretaceous -Palaeogene	Lefipan, Salamanca and Bororo	Archangelsky, (1973), Baldoni & Askin, (1993), Volkheimer et al., (2007)
<i>Proxapertites operculatus</i> (Hammen) Hammen	Palaeocene	Bororó	Archangelsky, (1973)
<i>Proxapertites</i> spp	Palaeocene	Bororó	Volkheimer et al., (2007)
<i>Spinizonocolpites hialinus</i> Archangelsky et Zamaloa	Palaeocene	Salamanca and Bororó	Archangelsky & Zamaloa, (1986)
<i>Sabalpollenites</i> sp.	Palaeocene	Salamanca	Archangelsky, (1973)
<i>Spinizonocolpites</i> sp.	Cretaceous	Lefipan, Salamanca and Bororó	Archangelsky, (1973), Baldoni & Askin, (1993), Volkheimer et al., (2007)
Salta Group Basin			
<i>Spinizonocolpites</i> sp.	Palaeocene	Mealla	Quattrocchio, et al., (1997, 2005)
	Palaeocene	Tunal	Volkheimer et al., (2006)
Colorado Basin			
<i>Arecipites minutiscabratus</i> McIntyre 1968	Upper Cretaceous (Maastrichtian) – Paleocene (Danian)	Lefipán	Barreda et al. (2012)
<i>Arecipites</i> sp.	Upper Cretaceous (Maastrichtian) – Paleocene (Danian)	Lefipán	Barreda et al. (2012)
<i>Longapertites aff. vaneendenburgi</i> Geermerad Hooping & Muller 1968	Upper Cretaceous (Maastrichtian) – Paleocene (Danian)	Lefipán	Barreda et al. (2012)
<i>Spinizonocolpites hialinus</i> Archangelsky & Zamaloa 1986	Upper Cretaceous (Maastrichtian) – Paleocene (Danian)	Lefipán	Barreda et al. (2012)
<i>Monosulcites minutiscabratus</i> McIntyre 1968	Palaeocene	Pedro Luro	Quattrocchio, et al., (2000), Ruiz & Quattrocchio, (1997)
Santa María Basin			
<i>Arecipites</i> sp	Neogene (Upper Miocene)	Chiquimil	Mautino et al. (1997), Mautino & Anzótegui (2002)
<i>Arecipites asymmetricus</i> (Frederiksen) Frederiksen 1983	Neogene (Upper Miocene)	Chuquimil	Mautino & Anzótegui (2002)
<i>Monosulcites</i> sp	Neogene (Upper Miocene)	Chiquimil	Mautino et al. (1997)

650 species, and include massive tree palms, undergrowth palms, and acaulescent palms, but they are better known for their spiny and climbing members: the rattans (Baker et al., 2000). Among them, the genus *Salacca* has twenty three species (Govaerts et al., 2015; Zumaidar et al., 2014) distributed from East of Himalaya to South-central China and West of Malesia (Govaerts et al., 2015).

The plants which produced the palynological assemblages of the Springhill, Piedra Clavada and Kachaika formations may have developed in a hot and humid climate, similar to the conditions present in tropical areas today (Barreda and Archangelsky, 2006). The presence of pollen tetrads comparable to that of the extant genus *Salacca* (Calamoid subfamily) reinforces this hypothesis.

These data agree with the information provided by the continental deposits of the Piedra Clavada Formation. The macrofossils include a broad range of ferns (*Nathorstia alata* Halle, *Gleichenites sanmartinii* Halle, *Cladophlebis* Brongniart and *Sphenopteris* Brongniart), conifers (*Brachyphyllum* Brongniart, *Elatocladus* Halle, *Araucarites* Presl and *Athrotaxis ungeri* Florin) and magnoliophyte leaves (Carrizo et al., 2011). In other ways, the palynological assemblages in Piedra Clavada show abundance of Schizaeaceae, Matoniaceae, Marsiliaceae, Salviniaceae, Isoetaceae, Cheirolepidiaceae, Araucariaceae and Taxodiaceae (Del Fueyo et al., 2007; Archangelsky et al., 2008; Villar de Seoane and Archangelsky, 2008; Archangelsky, 2009). The records of plant assemblages (macrofossils and palynomorphs) suggest the existence of a template to tropical humid forest during the deposition of the Piedra Clavada Formation, and the presence of palms strengthens this hypothesis.

On the other hand, the small dimensions and the spiny nature of *Spinizonocolpites* are interesting with respect to the pollinator type (Hesse, 2000; Sannier et al., 2009). The association insect-plant and pollination has been inferred to Mesozoic seed plants (Labandeira et al., 2007), even in early Magnoliophytæ (Hu et al., 2008). Furthermore, ornamented grains and the apparent absence of wind in dense and humid forests are also associated with biotic pollination (Hu et al., 2008; Whitehead, 1969). These conditions were inferred for the Piedra Clavada Formation, where the small size and spiny nature of the pollen grains (*Spinizonocolpites*-type) could be related to an entomophilous pollination.

In the box plot (Fig. 7) are represented several species of fossil and extant pollen grains of *Spinizonocolpites*, *Nypa*, *Korthalsia* and *Salacca*. This box plot suggests the existence, at least, of three groups: 1).

Group A, that comprise tiny pollen grains with a small range between 14 µm and 28 µm (*Salacca clemensiana*, *Salacca secunda*, *Spinizonocolpites spinulosus*); 2). Group B, is characterized by pollen grains with a range comprised between 21 µm and 58 µm (*Korthalsia* spp., our *Spinizonocolpites*-type tetrad, *Spinizonocolpites perspinosus*, *Spinizonocolpites hialinus*, *Spinizonocolpites echinatus*, *Spinizonocolpites intrarugulatus*, *Spinizonocolpites pengchiahsuensis*, *Spinizonocolpites-Complex*, *Spinizonocolpites indicus*, *Spinizonocolpites baculatus*, *Spinizonocolpites breviechinatus*, *Spinizonocolpites bulbospinosus*, *Spinizonocolpites wodehousei*); 3). Group C, with bigger pollen grains with a diameter of 40 µm–92 µm (*Nypa fruticans*, *Spinizonocolpites adamanteus*, *Spinizonocolpites pachyexinatus*, *Spinizonocolpites grandis*, *Spinizonocolpites sp. A*).

The groups A and B can be clustered to include the living species of Calamoids palms, and some species of *Spinizonocolpites*. The taxa of Group C include *Nypa* and allied taxa. At this point of our knowledge a revision of the genus *Spinizonocolpites* and allied taxa is needed, mainly with respect to their botanical affinity. The eventual link between *Spinizonocolpites* and *Nypa* may be equivocal in the interpretation of palaeoenvironmental conditions in which the pollen is found.

7. Conclusions

Spinizonocolpites is commonly considered as related to the extant palm *Nypa*, which produces tetragonal tetrads. Thus, the form of the tetrads of the Early Cretaceous Patagonian species (tetrahedral tetrad) suggests different botanical affinity and probably justifies with further investigations its segregation from the genus *Spinizonocolpites*. On the other hand, the Patagonian tetrads have features close to extant calamoid palms (e.g. *Salacca*). This may suggest an early diversification of palms in the Early Cretaceous, and reinforce the proposal of an ancient origin of Monocots at the beginning of the Cretaceous. Probably, the oldest Mesozoic palms are present in a low number masked by a flora dominated by conifers, cycads, Bennettiales, pteridosperms and ferns. Our report presents the earliest record (Lower Cretaceous) of spiny tetrads with unequivocal palm affinity (*Spinizonocolpites*-type) from high latitudes.

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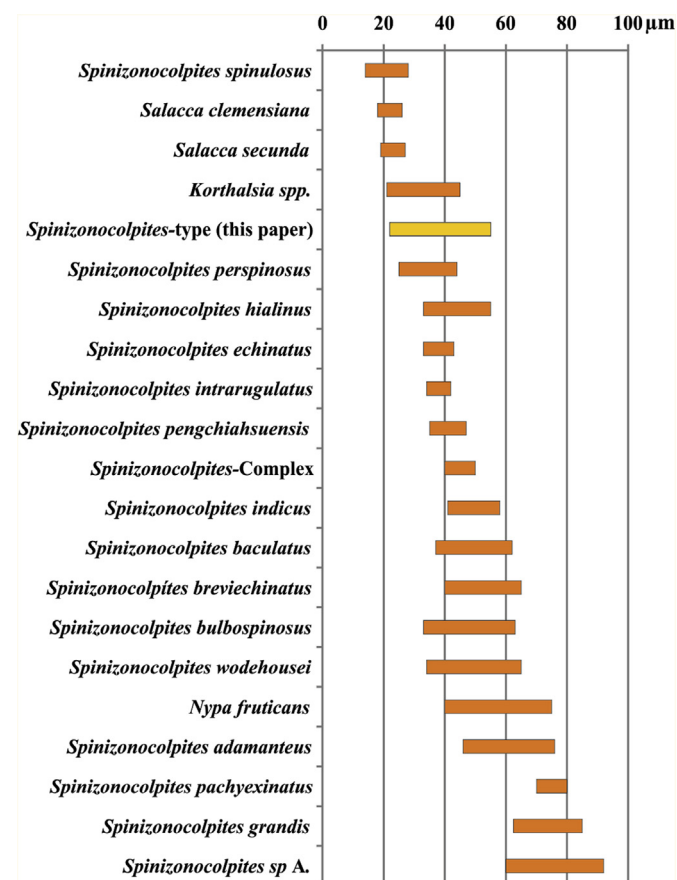


Fig. 7. The box plot shows the differences in average of length between some extant and fossil palm pollen grains.

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