

Salvinialean megaspores in the Late Cretaceous of southern Patagonia, Argentina

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We report here two megaspores species related to the aquatic ferns of the order Salviniales from the Late Cretaceous Mata Amarilla Formation (Austral Basin), southern Santa Cruz Province, Argentina. We identified the species *Arcellites disciformis* and *Balmeisporites* cf. *B. holodictyus*. The presence of *A. disciformis*, in particular, is significant not only because it represents the first record for the Southern Hemisphere, indicating a bi-hemispheric distribution for the species, but also because it increases the diversity of this genus in Patagonia. The new findings of salvinialean megaspores highlight the importance of water ferns in the Late Cretaceous aquiferous environments of southern South America. The common occurrences of *Arcellites* and *Balmeisporites*, whether in shallow, fresh or brackish water facies, indicates aquatic paleoenvironment of the Mata Amarilla Formation, as was inferred also from the sedimentological evidence. Their presence also indicates that the lower and middle levels of the Mata Amarilla Formation can be attributed to the megaspore Zone M3 (Albian–Cenomanian) defined for the Cretaceous of Patagonia.

Key words: Salviniales, Hydropteridales, *Arcellites*, megaspores, Cenomanian, South America, Argentina.

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Introduction

Water ferns are a monophyletic clade of heterosporous ferns consisting of two extant families, Marsileaceae and Salviniaceae, placed in the order Salviniales (Smith et al. 2006) or Hydropteridales (Rothwell and Stockey 1994; Yamada and Kato 2002). They have a relatively simple vegetative structure coupled with a highly specialized reproductive arrangement, and live as rooted plants in moist or flooded places or as free-floating plants. Marsileaceae include three extant genera: *Marsilea* Linnaeus, 1753, *Pilularia* Linnaeus, 1753, and *Regnellidium* Lindman, 1904, and Salviniaceae comprise two extant genera: *Azolla* Lamarck, 1783, and *Salvinia* Séguier, 1754. These families are not easily related to the larger clade of leptosporangiate ferns, because the adaptation to the aquatic habitat has deeply influenced the morphology of the sporophyte and spores (Tryon and Tryon

1982; Tryon and Lugardon 1991). Megagametophytes are enclosed within the megaspores (generally dispersed in water), which have a complex spore wall stratification, including a specialized epispore (Tryon and Tryon 1982; Tryon and Lugardon 1991).

Salviniales have a widespread fossil record since the Late Jurassic, based both on macro and microfossils, including megaspores with their respective microspores in organic connection (e.g., Cookson and Dettmann 1958; Ellis and Tschudy 1964; Collinson 1980, 1991, 2001, 2002; Archangelsky et al. 1999; Lupia et al. 2000; Yamada and Kato 2002; Vajda and McLoughlin 2005; Villar de Seoane and Archangelsky 2008; Batten et al. 2011a, b; Cúneo et al. 2013).

In Patagonia, salvinialean megaspores have been widely recorded in Early Cretaceous units such as: the Springhill Formation (Berriasian–Barremian) (Baldoni and Taylor 1985; Baldoni and Batten 1997), the Baqueró Group (Aptian) (Gammero 1975; Taylor and Taylor 1988; Villar de Seoane

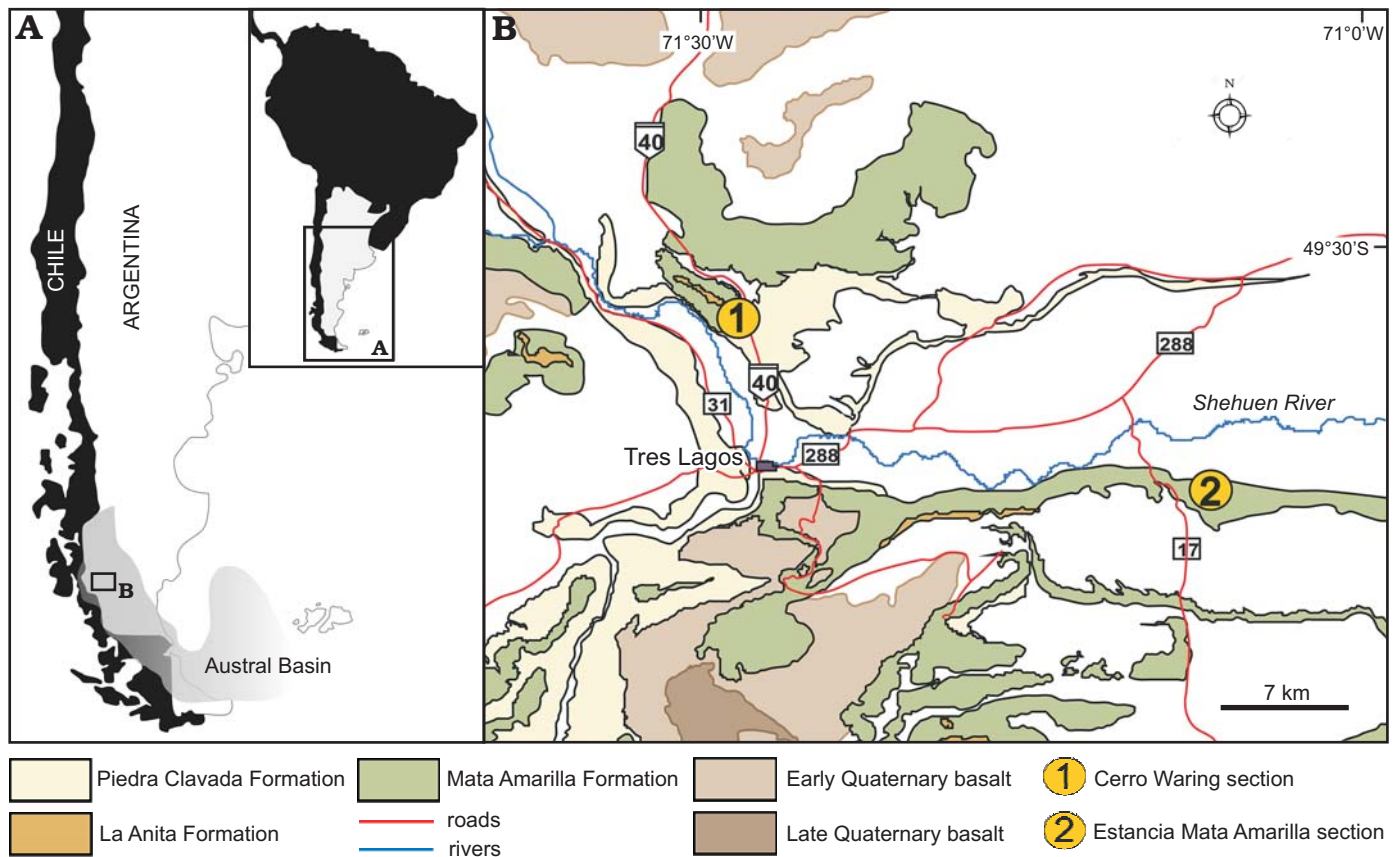


Fig. 1. Geographic (A) and geological (B) maps of the studied area (Tres Lagos Town, Santa Cruz Province, Argentina), showing the location of the studied sections (modified from Varela 2011).

1988; Archangelsky and Villar de Seoane 1989, 1990, 1991), the Kachaiké Formation (Albian) (Baldoni 1987; Baldoni and Taylor 1987, 1988; Baldoni and Batten 1991; Villar de Seoane and Archangelsky 2008) and the Piedra Clavada Formation (Albian) (Villar de Seoane and Archangelsky 2008). Records from the Late Cretaceous are mainly restricted to the Campanian and Maastrichtian (Stough 1968; Archangelsky et al. 1999; Marensi et al. 2004; Cúneo et al. 2013, 2014; Hermsen et al. 2014)

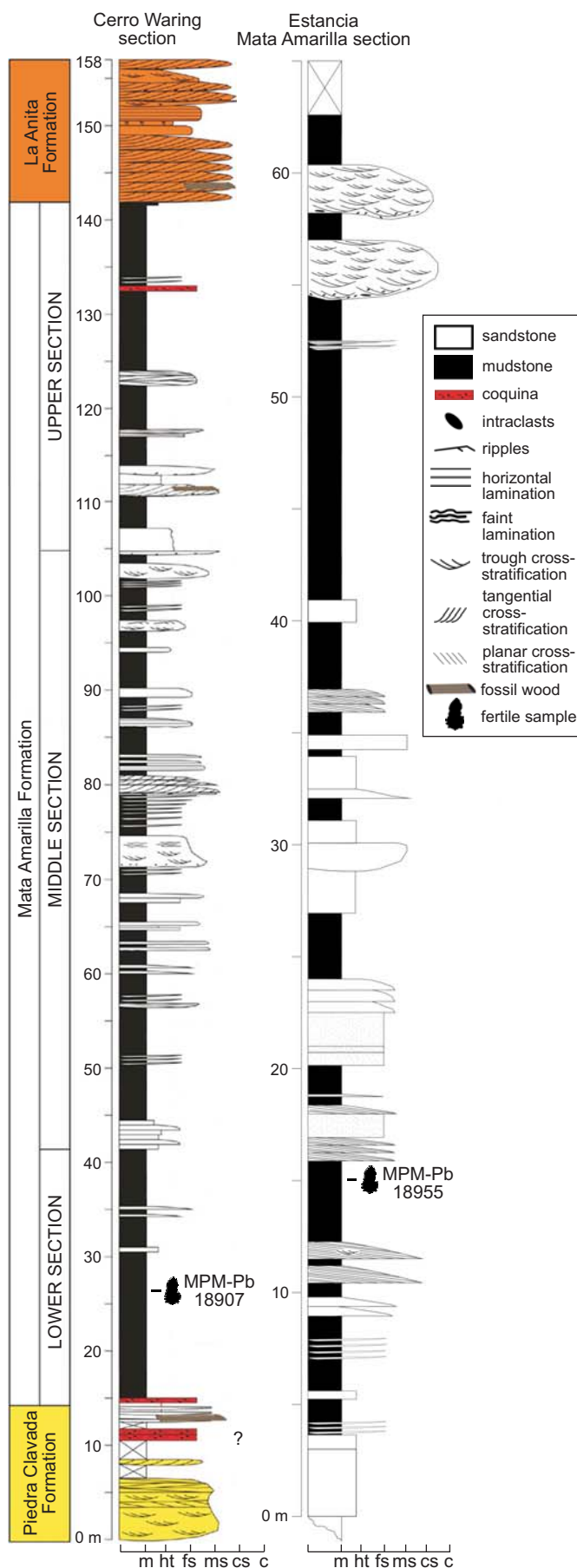
The Mata Amarilla Formation (Feruglio in Fossa Mancini et al. 1938; Leanza 1972) crops out around the town of Tres Lagos in southern Santa Cruz Province (Fig. 1), transitionally overlies the Piedra Clavada Formation (middle–late Albian; Riccardi et al. 1987; Archangelsky et al. 2008; Poiré et al. 2017) and is unconformably overlain by the La Anita Formation (Campanian; Varela et al. 2012a). It comprises three sections: lower, middle and upper (Varela et al. 2011, 2012a, b) that grade from fluvial to estuarine facies.

Here we report the presence of megaspores related to aquatic ferns from the lower and middle sections of the Mata Amarilla Formation at Cerro Waring (S49°31'16.8" W71°29'7.7") and Estancia Mata Amarilla (S49°37'5.9" W71°7'40.5") localities, southern Santa Cruz Province, Argentina (Figs. 1, 2). The paleobiogeographic and paleoenvironmental significance of these new fossil records is also discussed.

Institutional abbreviations.—CIG, Centro de Investigaciones Geológicas, La Plata, Argentina; CONICET, Consejo Nacional de Investigaciones Científicas y Técnicas; INIBIOMA, Instituto de Investigaciones en Biodiversidad y Medioambiente, San Carlos de Bariloche, Argentina; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MPM-Pb, Museo Regional Provincial “Padre Jesús Molina” Paleobotanical collection, Rio Gallegos, Argentina; UNCO, Universidad Nacional del Comahue, San Carlos de Bariloche, Argentina; UNLP, Universidad Nacional de La Plata, La Plata, Argentina.

Geological setting

The Austral (or Magallanes) Basin, is located on the southwestern end of the South American Plate (Fig. 1) and it is bordered to the south by the Scotia Plate covering an area of approximately 230,000 km². In the studied area, the Austral Basin underwent three main tectonic stages (Varela 2014 and references therein): (i) a rift stage; (ii) a thermal subsidence stage; and (iii) a foreland stage. The rifting stage is related to the break-up of Gondwana, grabens and half-grabens were formed and filled with volcanoclastic and volcanic rocks intercalated with epiclastic sediments of the El Quemado and Tobifera formations. Subsequently, the thermal subsidence



stage resulted in the deposition of the transgressive quartzose sandstone of the Springhill Formation, and the black mudstone and marl of the Río Mayer Formation. Towards the end of this stage, the Piedra Clavada Formation was deposited, representing a large passive-margin delta system. The foreland stage, in response to the regional change from extensive to compressive regime, resulted in the deposition of the continental Mata Amarilla Formation (Varela 2014). This unit is mainly composed of grey and blackish siltstone and claystone, alternating with whitish and yellowish-grey fine to medium grained sandstone (Varela et al. 2012b). Varela (2014) recognized three informal sections (lower, middle, and upper) on the bases of sedimentological and sequence stratigraphic analysis. The lower section consists of fine-grained intervals with paleosols interbedded with laminated shale and coquina, representing coastal plain and lagoon paleoenvironments. The middle section comprises sandstone and siltstone representing meandering fluvial channels and crevasse splay deposits (Varela 2011), intercalated with fine-grained floodplains and subordinate lacustrine deposits (Varela 2011). The upper section is dominated by fine-grained deposits, related to distal fluvial channels. U-Pb dating indicates a middle Cenomanian age (96.2 ± 0.7 Ma) for the middle section of the Mata Amarilla Formation (Varela et al. 2012a). Paleosol features and paleosol-derived climatic proxies suggest a subtropical temperate-warm ($12 \text{ }^\circ\text{C} \pm 2.1^\circ\text{C}$) and humid (1404 ± 108 mm/yr) climate with marked rainfall seasonality during the deposition of this unit (Varela et al. 2012b; 2018), in accordance with previous paleobotanical interpretations (Iglesias et al. 2007; Varela et al. 2016).

Material and methods

Two levels of the Mata Amarilla Formation contain well preserved water fern megaspores: level CW1-003 at the Cerro Waring section (sample MPM-Pb-18907), and level MAT3-MAL'A' at the Estancia Mata Amarilla section (sample MPM-Pb-18955). Rock samples were treated with traditional palynological techniques and the residues were sieved through 200 μm and 25 μm meshes. For light microscopy observations, residues were dehydrated with alcohol, and mounted in UV-curable acrylate (Noetinger et al. 2017). Slides were observed under a Leica DM500 microscope and photographed with a Leica ICC50 HD camera. Specimen locations are referred to by using England Finder coordinates between brackets. For scanning electronic microscopy (SEM) and transmission electronic microscopy (TEM) observations, individual megaspores were picked from the 200 μm residue, under a light microscope at $10\times$ magnifi-

Fig. 2. Stratigraphic sections of the Mata Amarilla Formation at Cerro Waring and Estancia Mata Amarilla localities, showing samples location. Abbreviations: c, conglomerate; cs, coarse sandstone; fs, fine sandstone; ht, heterolithic; m, mudstone; ms, medium sandstone.

cation. For SEM, specimens were mounted on a cover glass and coated with gold-palladium; observations were made under a Philips XL30 TMP microscope at the Electronic Microscopy Service of the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN). Ultrathin sections were made for TEM, and observed under a Jeol 1200 EX II from the Central Service of Electronic Microscope of the Faculty of Veterinary Science, National University of La Plata. The specimens are stored at the Museo Regional Provincial “Padre Jesús Molina”, Rio Gallegos, Santa Cruz Province (MPM-Pb). Terminology used for describing fossil megaspores and spore wall structure follows Batten et al. (2011b). In particular, for *Arcellites* we use the term acrolamella in the sense of Batten et al. (2011b), who restricted that word to the aggregation of leaf-like, commonly twisted segments that enclose the triradiate suture of the megaspores.

Systematic palaeontology

Division Monilophyta Pryer, Schuettpelz, Wolf, Schneider, Smith, and Cranfill, 2004

Class Polypodiopsida Cronquist, Takhtajan, and Zimmerman, 1966

Order Salviniiales Bartling in von Martius, 1835

Genus *Arcellites* (Miner, 1935) Ellis and Tschudy, 1964

Type species: *Arcellites disciformis* (Miner, 1935) Ellis and Tschudy, 1964; Cenomanian of the east coast of Disko Island, Greenland.

Arcellites disciformis (Miner, 1935) Ellis and Tschudy, 1964

Fig. 3.

1935 *Arcellites disciformis* sp. nov.; Miner 1935: 600, pl. 20: 61, 64–66. 1964 *Arcellites disciformis* (Miner, 1935); Ellis and Tschudy 1964: 75, pl. 1: 1–12, text-fig. 1.

Material.—16 specimens measured. Sample MPM-Pb-18907a (N40/1); MPM-Pb-18907b (R48/2); MPM-Pb-18907 SEM stub 1 (4 specimens), MPM-Pb-18907 SEM stub 2 (2 specimens), MPM-Pb-18907 SEM stub 3 (4 specimens), and MPM-Pb-18907 TEM (4 specimens). Cenomanian of Patagonia, Argentina. Cerro Waring locality, Mata Amarilla Formation.

Description.—Trilete megaspore with spherical body and long acrolamella at proximal face, covering the trilete mark (Fig. 3A₁, B₁). Megaspore body with 25 to 40 short appendages regularly distributed, with reticulated ends (Fig. 3C₂). Body sculpture foveolate (Fig. 3A₂, B₂). Fovea perpendicular to surface (Fig. 3B₃), rounded between appendages, and ovate to slender at their bases (Fig. 3A₂). Acrolamella composed of leaf-like appendages twisted along their length, with fimbriate margins and smooth surface (Fig. 3C₁). In SEM and TEM, the megaspore wall shows a tripartite structure composed of an outer exoexine, an inner exoexine and an intexine

(Fig. 3B₃, D). In TEM, the outer exoexine presents a coarsely granular aspect (Fig. 3D₁), with granules that range in diameter from 0.3–0.4 µm. Towards the surface, outer exoexine becomes massive, and numerous pits penetrate it perpendicularly giving a palisade-like appearance. The inner exoexine is loosely and finely granulated (granules <0.2 µm in diameter). The intexine presents the most solid aspect of the three wall layers, and at high magnifications ultra-thin and irregular channels (<0.1 µm in diameter) are observed (Fig. 3D₂).

Dimensions.—Total length (body and acrolamella) 367–378 µm, body diameter 255–278 µm (with appendages), length of appendages 21–51 µm, width of appendages 21.2–36.3 µm, fovea 0.9–2.5 × 0.9–2.2 µm (1.5 × 2.7 µm at base of appendages), acrolamella length 165.7–196.6 µm, acrolamella width 111–155 µm, exine thickness 10.7–18.3 µm, outer exoexine thickness 6–8 µm, inner exoexine thickness 2.3–5.7 µm, intexine thickness 2.4–4.6 µm.

Remarks.—*Arcellites disciformis* (Miner, 1935) Ellis and Tschudy, 1964 and *Arcellites hexapartitus* (Dijkstra, 1951) Potter, 1963 share a similar general morphology; Batten et al. (1996) compared and contrasted these species and listed a series of characters useful to separate them. *Arcellites disciformis* is characterized by the presence of: (i) leaf-like segments of the neck tightly twisted against each other, (ii) leaves of acrolamella with well-developed fimbriate margins, (iii) megaspore wall surface profusely pitted, (iv) appendages with reticulate tips and absence of surface swellings of the exoexine. The Patagonian specimens conform to the diagnosis of *Arcellites disciformis* and present all the morphological features that characterized the species (Hueber 1982; Batten et al. 1996).

The Argentinean specimens have similar dimensions to those reported for the Barremian–Aptian of Virginia, USA (Hueber 1982) and for the Albian–Cenomanian of Maryland, USA (Lupia 2015). However, they are smaller than those described for the Albian–Cenomanian of the Denver Basin, central USA (Ellis and Tschudy 1964) and for the Cenomanian of Alberta, Canada (Singh 1983). Differences in size may be related to dehydration during processing as previously noted by Hueber (1982).

Mays (2011) reported the presence of *A. disciformis* for the Cenomanian of Chatham Islands, New Zealand, but the illustrated specimens do not show the main morphological features that characterized the species (Batten et al. 1996) and might be related to *A. hexapartitus*.

Stratigraphic and geographic range.—Barremian–Cenomanian of USA (Schemel 1950; Hall 1963; Potter 1963; Ellis and Tschudy 1964; Hall and Peake 1968; Hueber 1982; Kovach and Dilcher 1988; Lupia 2015), Barremian–Cenomanian of Canada (Singh 1964, 1971, 1983; Hopkins and Sweet 1976; Sweet 1979), Albian–Cenomanian of Greenland (Miner 1935; Koppelhus and Pedersen 1993; Batten et al. 1996), Aptian–Cenomanian of Sudan (Kaska 1989), Turonian of France (Colin 1975), Aptian of Germany (Schultz and Noll 1987), Cenomanian of Patagonia (this work).

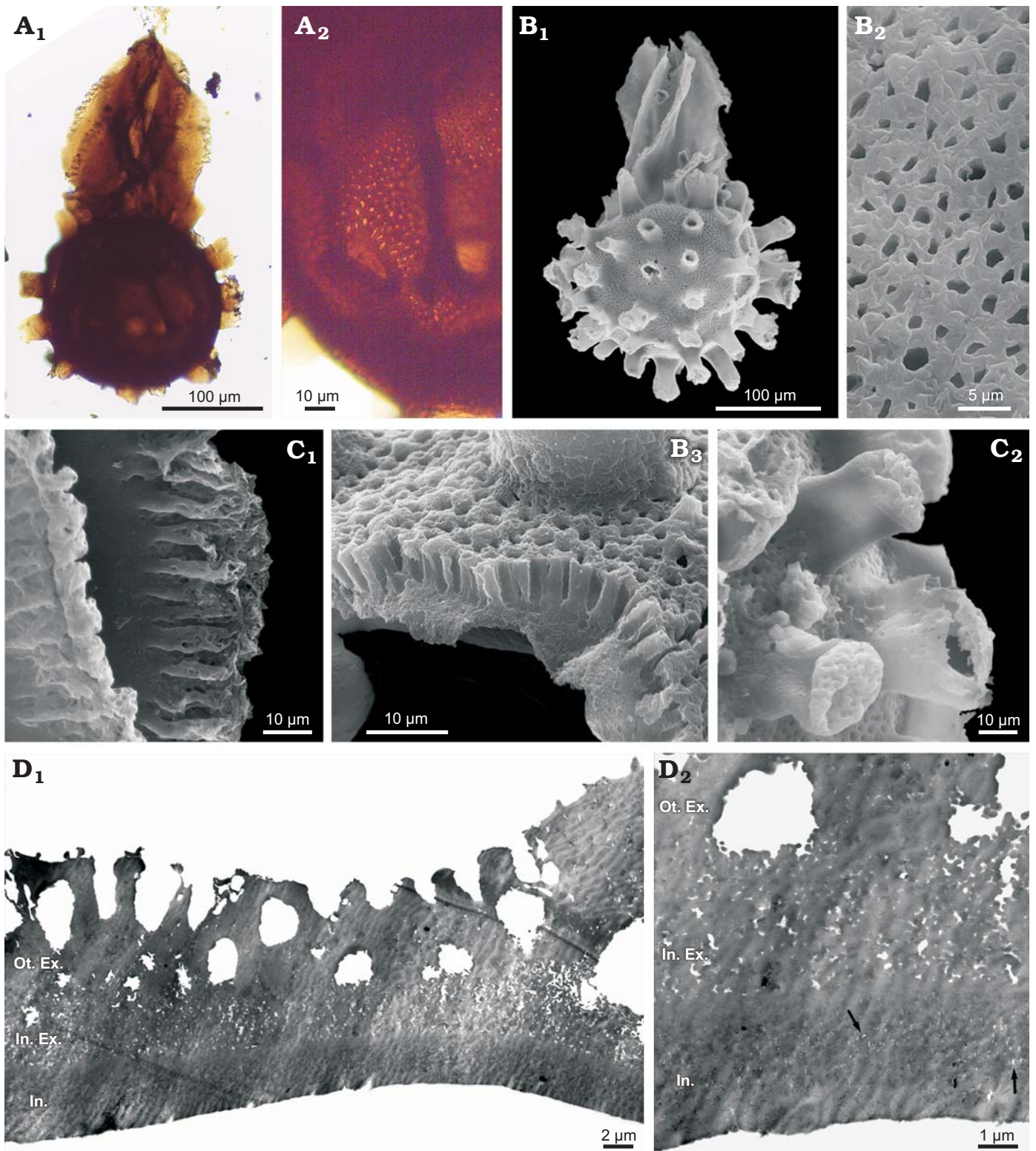


Fig. 3. Megaspores of the water fern *Arcellites disciformis* (Miner, 1935) Ellis and Tschudy, 1964; Cenomanian, town of Tres Lagos, Argentina. **A.** MPM-Pb-18907a (N40/1), general view under light microscope (A_1), a detail of the pitted pattern (A_2). **B.** MPM-Pb-18907 SEM stub 1, general view under SEM (B_1), a detail of pitted surface under SEM (B_2), a detail of wall in cross-section under SEM, showing the palisade structure of outer exoexine (B_3). **C.** MPM-Pb-18907 SEM stub 3, detail of acrolamella under SEM, showing leaves with well-developed fimbriate margins (C_1), detail of the reticulated tips of appendages (C_2). **D.** MPM-Pb-18907 TEM, body of the spore showing wall-layers under TEM, with coarsely granulated outer exoexine, loosely and finely granulated inner exoexine and massive intexine (D_1); detail showing ultra-thin channels (arrows) of intexine (D_2). Abbreviations: Ot. Ex., outer exoexine; In. Ex., inner exoexine; Int., intexine.

Genus *Balmeisporites* (Cookson and Dettmann, 1958) Dettmann, 1995

Type species: Balmeisporites holodictyus Cookson and Dettmann, 1958; Albian of Robe Bore, South Australia.

Balmeisporites cf. *B. holodictyus* Cookson and Dettmann, 1958

Fig. 4.

1958 *Balmeisporites holodictyus* sp. nov.; Cookson and Dettmann 1958: 42, pl. 2: 1–6, text-fig. 3.

Material.—32 specimens measured. MPM-Pb-18907a (J53/3, H32/4, K49/1, Q49/1, F39, D28/2, C33/3, C30/2, B40/2, H32/4, R33); MPM-Pb-18907b (Z33/4, W39/4, U49/2, J37/1, C38/2, E36/2); MPM-Pb-18907 SEM stub 1 (5 specimens); MPM-Pb-18955a (M35/3, W43, Y44/2, Y34/3); MPM-Pb-18955b (V44/3, J52/1, N42/3); MPM-Pb-18955c (G25/1); MPM-Pb-18955d (Z45, H25/1). Cenomanian of Patagonia, Argentina. Cerro Waring and Estancia Mata Amarilla localities, Mata Amarilla Formation.

Description.—Trilete megaspore with round to elliptical body. Laesurae with membranous, highly elevated lips (Fig. 4A, B). Lips finely granulated (Fig. 4C). Megaspore surface irregularly reticulate. Lumina polygonal to irregular in shape, larger near the equator (Fig. 4A, B), sculpture inside lumina scabrated. Muri of the reticulum narrow and low (Fig. 4B).

Dimensions.—Total length (body and lips) 125–197 μm , body diameter 90–142.9 μm , lumina diameter 7–20 μm , reticulum wall thickness 1–3.5 μm , length of lips 36–45 μm , width of lips 80–136 μm .

Remarks.—The Patagonian specimens broadly fit with the general diagnosis of *B. holodictyus* (Cookson and Dettmann 1958; Dettmann 1995) but differ in lacking the three wing-like outgrowths in each radial equatorial region. Some specimens show variations in the development of the reticulum (Fig. 4D, E), a feature also reported for specimens from the Aptian–Albian of Australia (Tosolini et al. 2002). Bearing in mind that we only recovered few poorly preserved specimens, we temporarily retain these megaspores within *B.* cf. *B. holodictyus* (Fig. 4D, E), although we cannot rule out that they belong to a different species. This species has been widely reported from the Barremian to Danian around the globe (Dettmann 1995).

Discussion

The record of *Arcellites* and *Balmeisporites* in the Cenomanian of southern Patagonia enlarges the distribution of salvinialean megaspores in the area. In particular, the presence of *A. disciformis* is significant because it represents the first Southern Hemisphere record; all previous reports being restricted to the Northern Hemisphere (Fig. 5). This new record indicates a bi-hemispheric distribution for the species. The genus *Arcellites* was previously represented in

Patagonia by four species: *A. santacruzensis* Baldoni, 1987; *A. humilis* Villar de Seoane and Archangelsky, 2008; *A. pentagonalis* Villar de Seoane and Archangelsky, 2008; and *Arcellites* sp. A in Villar de Seoane and Archangelsky, 2008, ranging from Albian to Cenomanian in age (Baldoni 1987; Baldoni and Taylor 1988; Villar de Seoane and Archangelsky 2008). The new species record increases the diversity of the genus for the Cretaceous of Patagonia.

Arcellites has been related to Salviniales on the bases of both general morphology and association with microspores of *Crybelosporites* Dettmann, 1963. The acrolamella of *Arcellites* with six twisted segments is broadly comparable to that of recorded in megaspores of some extant members of Marsileaceae (*Regnellidium* and *Pillularia*) and the closely related extinct genus *Molaspora* Schemel, 1950 (Lupia et al. 2000; Cúneo et al. 2013; Friss et al. 2014). The wall ultrastructure of *Arcellites*, however, differs from that present in any extant species of Marsileaceae and, according to Collinson (1991), it may be related to an extinct family within Salviniales. Dispersed microspores of *Crybelosporites* have been related to aquatic ferns of Salviniales (Dettmann 1963), so that, the presence of microspores of *Crybelosporites* in the folds of the acrolamella of *Arcellites* species also suggests its relationship with the order (Cookson and Dettmann 1958; Hall 1963; Ellis and Tschudy 1964; Hall and Peake 1968; Hueber 1982; Li and Batten 1986; Tosolini et al. 2002; Lupia 2004, 2015; Friis et al. 2014). *Crybelosporites* is also associated with fossil megaspores of the genus *Molaspora*. Both taxa were found in situ in sporocarps related to *Regnellidium* in the Santonian of Georgia, USA (Lupia et al. 2000). The diversity and abundance of these megaspores in the Cretaceous of southern Patagonia is remarkable. The fact that *Crybelosporites* is related to both *Molaspora* and *Arcellites* supports evolutionary links between them, as well as with their parent plants (Zavialova and Batten 2018).

The presence of acrolamella and appendages resembling bladder-like swellings in *Arcellites* were interpreted as adaptations to floating and fertilization on the water surface (Ellis and Tschudy 1964). This was also supported by the common occurrences of *Arcellites* either in shallow fresh or brackish water facies (Cookson and Dettman 1958; Ellis and Tschudy 1964; Tosolini et al. 2002).

Balmeisporites is a widespread Cretaceous genus with a continuous history ranging from the Barremian to the Danian, and with a cosmopolitan distribution during the Albian–Cenomanian (Dettmann 1995). This genus was referred to a new fossil order of heterosporous plants following the finding of a fertile plant in the Cenomanian of western Siberia (Krasilov and Golovneva 2000), but this affinity needs to be revised. At present, most researchers have little doubt that *Balmeisporites* was derived from a water fern within the Salviniales, mainly on the bases of general morphology and spore wall characters (Hall 1974; Baldoni and Batten 1991; Dettmann 1995; Villar de Seoane and Archangelsky 2008; Lupia 2011).

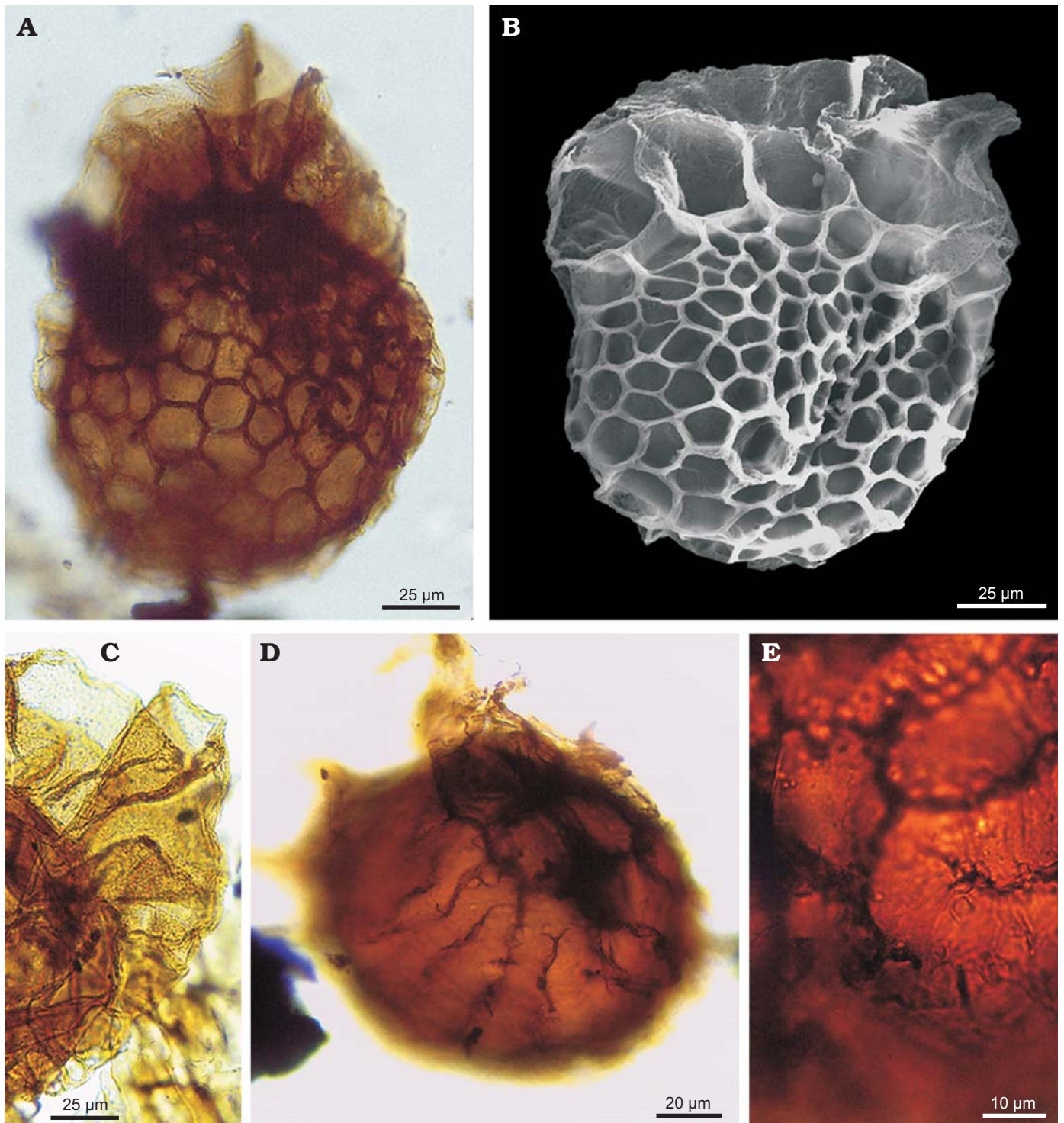


Fig. 4. Megaspores of the water fern *Balmeisporites cf. B. holodictyus* Cookson and Dettmann, 1958; Cenomanian, town of Tres Lagos, Argentina. **A.** MPM-Pb-18907a (H32/4), general view under light microscope. **B.** MPM-Pb-18907 SEM stub 1, general view under SEM, showing the larger reticulum in the equatorial region. **C.** MPM-Pb-18907a (Q49/1), detail of finely granulated lips. **D.** MPM-Pb-18907a (F39), general view of one individual with variations in reticulum development. **E.** MPM-Pb-18907a (J53/3), detail of the variations in reticulum development.

Three chronostratigraphic zones were defined for the Berriasian–Cenomanian of southern Patagonia characterized by its megaspore content (Villar de Seoane and Archangelsky 2008). These are: M1 (Berriasian–Barremian), M2 (Aptian), and M3 (Albian–?Early Cenomanian). Based

on the presence of these species, the lower and middle levels of the Mata Amarilla Formation may be referred to the Zone M3, which is characterized by the presence of *B. holodictyus*, several species of *Arcellites*, along with lycopsid megaspores. Records of *A. disciformis* are mostly restricted

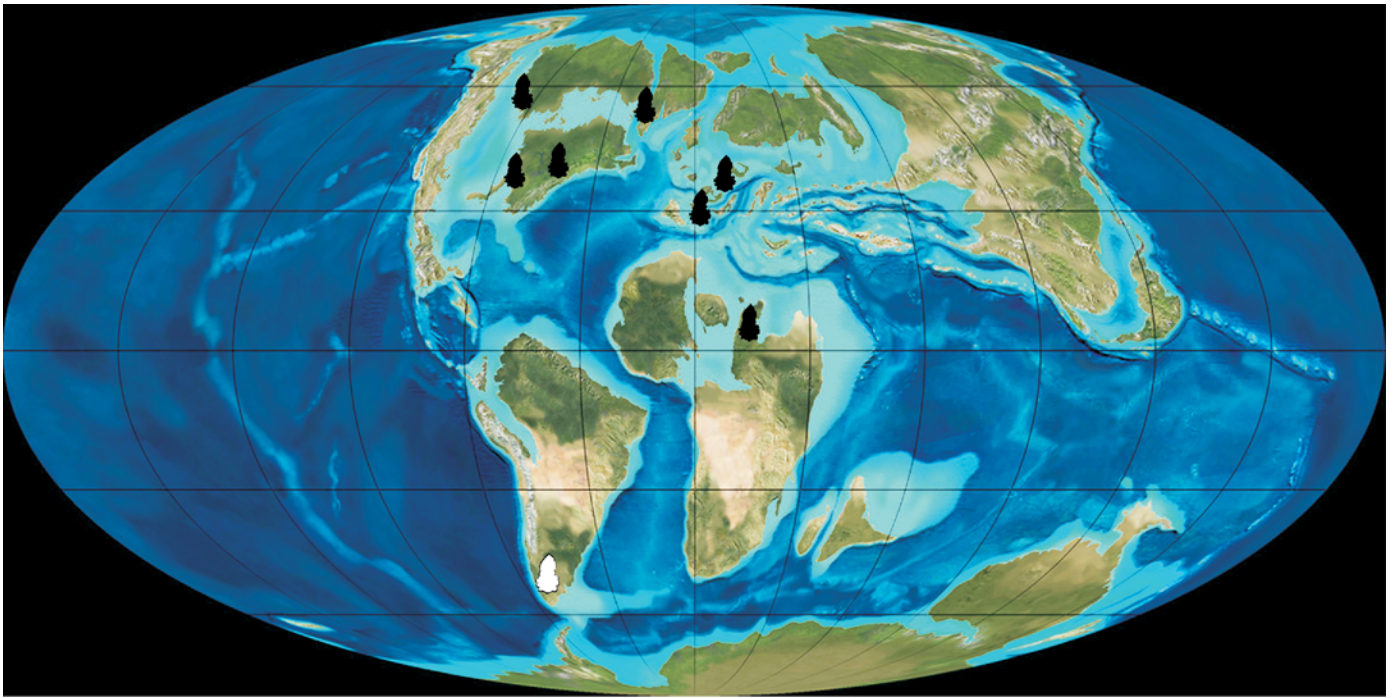


Fig. 5. Paleogeographic map of the Late Cretaceous (modified from Blakey 2010) showing the known distribution of *Arcellites disciformis* (black symbols), and the new Patagonian record (white symbol).

to the Albian–Cenomanian in the Northern Hemisphere (except for the Barremian–Aptian of Virginia, USA), suggesting that it may have potential as biostratigraphic marker for the Cenomanian in Argentina. The presence and abundance of these water ferns in the lower and middle sections of the Mata Amarilla Formation supports a local aquatic paleoenvironment as was also suggested by sedimentological evidence (Varela 2011), with fresh or brackish water bodies under warm and humid conditions.

Conclusions

The new record of *Arcellites disciformis* and *Balmeisporites* cf. *B. holodictyus* in the Mata Amarilla Formation extends the distribution of water ferns in the Cenomanian of southern Patagonia. In particular, the finding of *A. disciformis* is important since it represents the first record of the species for the Southern Hemisphere; all previous reports came from the Northern Hemisphere. This new finding supports a bi-hemispheric distribution for the species and also increases the diversity of the genus *Arcellites* in the Cretaceous of Patagonia.

These new findings allow correlating the lower and middle sections of the Mata Amarilla Formation with the megaspore Zone M3 (Albian–Cenomanian) defined for southern Patagonia. They also support an aquatic environment for this unit with fresh or brackish water bodies developed under warm and humid conditions.

Overall, the present findings enlarge the importance of salvinealean megaspores in Late Cretaceous ecosystems of

southernmost South America. Further investigation in yet unexplored areas would help to better understand the evolutionary history of these water ferns.

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