Review of Palaeobotany and Palynology 290 (2021) 104428

Contents lists available at ScienceDirect

Review of Palaeobotany and Palynology

journal homepage: www.elsevier.com/locate/revpalbo

Research papers

Water fern spores (Salviniales) from the Late Cretaceous of Patagonia, Argentina

Facundo De Benedetti [a,*], María C. Zamaloa [a], María A. Gandolfo [b], Néstor R. Cúneo [a]

[a] Museo Paleontológico Egidio Feruglio, Consejo Nacional de Investigaciones Científicas y Técnicas, Avenida Fontana 140, 9100 Trelew, Chubut, Argentina
[b] L. H. Bailey Hortorium, Plant Biology Section, School of Integrative Plant Science, Cornell University, Ithaca, New York 14853, USA

ARTICLE INFO

Article history:
Received 20 December 2020
Received in revised form 9 April 2021
Accepted 10 April 2021
Available online 14 April 2021

Keywords:
Heterospory
Late Cretaceous
Megaspore
Microspore
Patagonia
Salviniales

ABSTRACT

We describe a water fern spore assemblage from the Maastrichtian La Colonia Formation, Chubut Province, Patagonia, Argentina. The assemblage includes three species of *Azolla* (*A. andreisii* sp. nov., *A. coloniensis*, and *A.* sp. 1), two species of *Azollopsis* (*A. intermedia* and *A. tomentosa*), *Crybelosporites pannuceus*, *Gabonisporis cristata*, *Ghoshispora* sp., *Grapnelispora loncochensis*, two species of *Molaspora* (*M. lobata* and *M. reticulata*), and *Paleoazolla patagonica*. *A. tomentosa*, *A. intermedia*, *G. cristata*, and *M. reticulata* are recorded for the first time in the Southern Hemisphere. *Ghoshispora* sp. constitutes the southernmost record of the genus and its first mention for Argentina. In addition, the genus *Azollopsis* is emended to include megaspore apparatuses with more than one megaspore. This water fern spore assemblage is one of the most diverse so far known for South America and substantiates the significant radiation that aquatic ferns underwent worldwide at the end-Cretaceous. Furthermore, it also implies that the presence of widespread suitable paleoenvironments allowed the establishment and rapid evolution of these plant communities in Patagonia.

1. Introduction

Heterosporous water ferns are a monophyletic group that includes two families, Marsileaceae Mirbel and Salviniaceae Martinov, within the order Salviniales Link (Smith et al., 2006; PPG I, 2016). Marsileaceae encompasses the extant genera *Marsilea* L., *Regnellidium* Lindm., and *Pilularia* L. whereas Salviniaceae comprises two extant genera, *Azolla* Lam. and *Salvinia* Ség. (Tryon and Lugardon, 1991; Nagalingum et al., 2006; Smith et al., 2006).

The fossil record of Salviniales extends from the Late Jurassic or earliest Cretaceous to the present (Collinson, 1991, 2001; Yamada and Kato, 2002) and includes macro- and microfossils, although it is better known from dispersed megaspores and microspores (Kovach and Batten, 1989; Batten and Kovach, 1990; Collinson et al., 2013; De Benedetti et al., 2020). Based mainly on the Northern Hemisphere record, it seems that this monophyletic clade evolved during the Mesozoic and diversified in the Late Cretaceous at the same time as the flowering plants (Hall, 1974; Collinson, 1991; Lupia et al., 2000; Collinson et al., 2013; Estrada-Ruiz et al., 2018; Hermsen, 2019). In spite of that, the growing fossil record of Salviniales from the Cretaceous and Paleocene of southern Argentina (Patagonia), proves that the group was also well-represented in the Southern Hemisphere (Baldoni and Batten, 1997; Cúneo et al., 2013; De Benedetti et al., 2018, 2020, Hermsen et al., 2013, 2019; Puebla et al., 2014; Santamarina et al., 2018; Vallati et al., 2017; Villar de Seoane and Archangelsky, 2008, 2013).

In this contribution, we describe an exquisitely preserved and diverse water fern spore assemblage from the Maastrichtian La Colonia Formation, Chubut Province, Patagonia, Argentina (Fig. 1). The assemblage comprises previously described species reported in Cúneo et al. (2013), Hermsen et al. (2013), and De Benedetti et al. (2018, 2020), as well as a new species and new records for Argentina and the Southern Hemisphere. The past diversity of these Southern South American water ferns is assessed in the context of aquatic and semiaquatic paleoenvironments developed in Patagonia during Late Cretaceous times.

2. Materials and methods

2.1. Stratigraphy and paleontology

The La Colonia Formation outcrops at the central north of the Chubut Province, Patagonia, Argentina (Fig. 1, 1). Stratigraphically, the La Colonia Fm. overlies the fluvial deposits of the Campanian-Maastrichtian Puntudo Chico Formation at the study area of the Mirasol Chico Creek (Ardolino and Franchi, 1996; Anselmi et al., 2004). Overlying units include brackish paludal siliciclastic facies of the Paleocene Cerro Bororó Formation, the Paleocene-Eocene El Buitre Formation basalts, and Oligocene pyroclastic rocks of the Sarmiento Formation

* Corresponding author.
E-mail addresses: fdebenedetti@mef.org.ar (F. De Benedetti), magandolfo@cornell.edu (M.A. Gandolfo), rcuneo@mef.org.ar (N.R. Cúneo).

https://doi.org/10.1016/j.revpalbo.2021.104428
0034-6667/

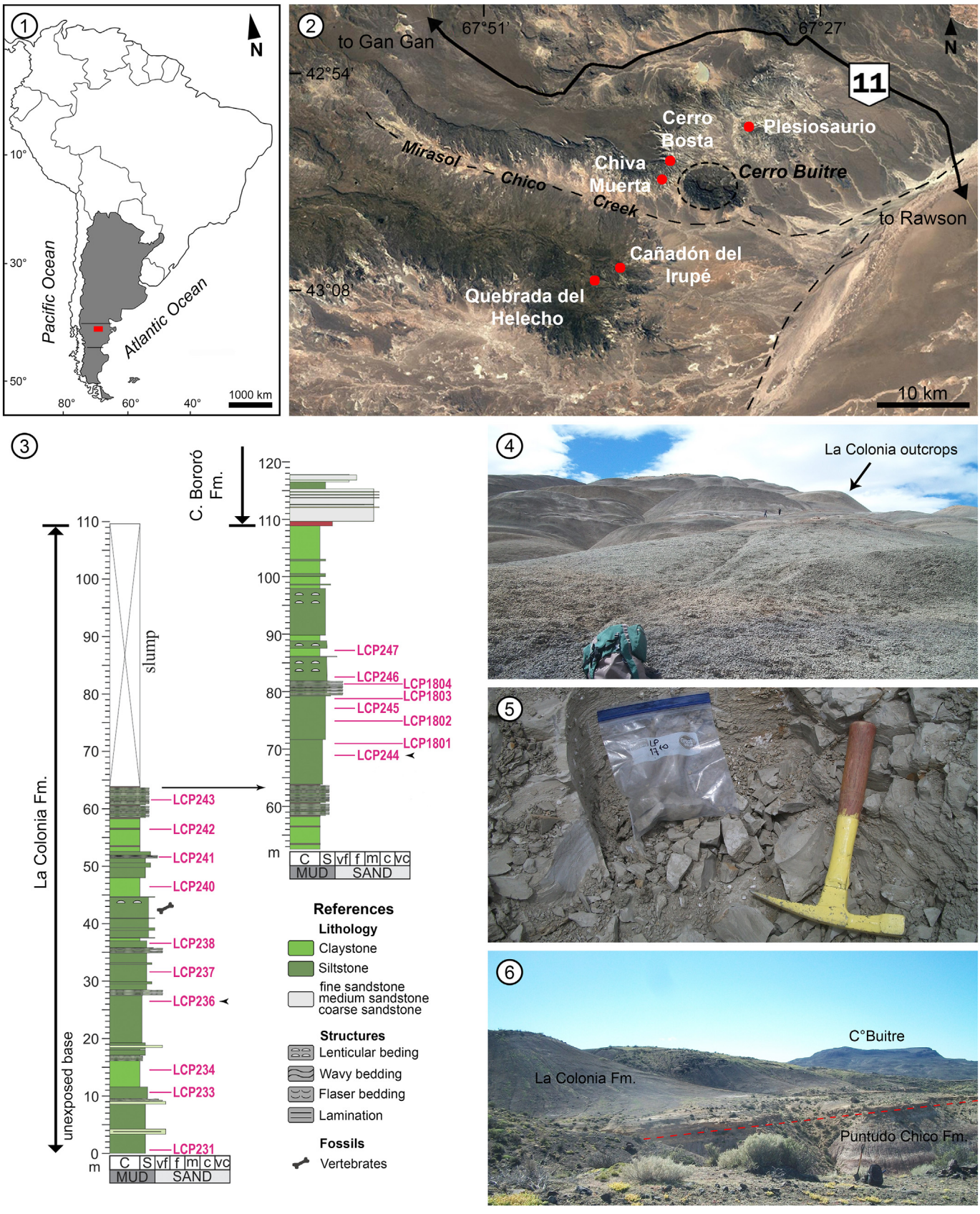
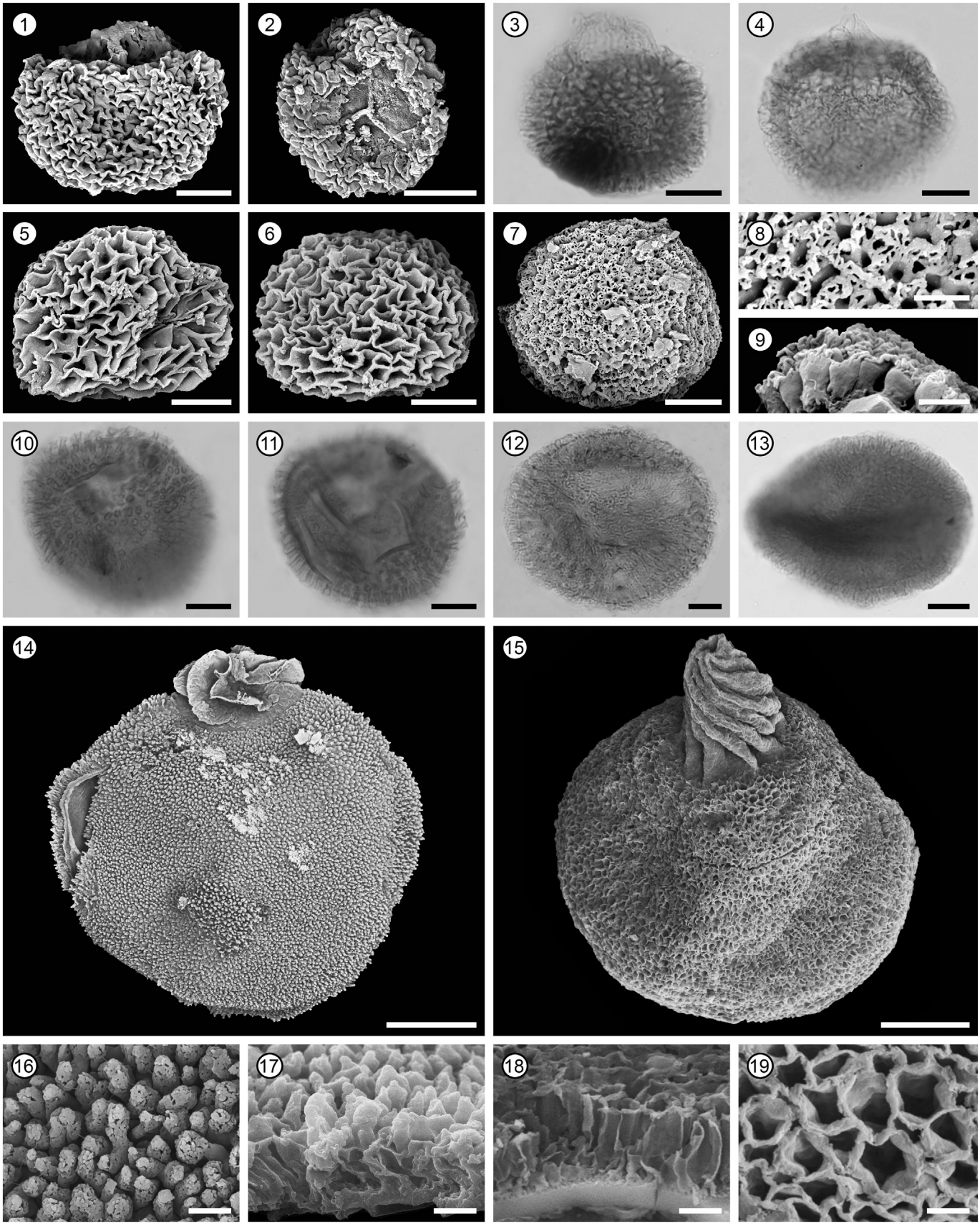


Fig. 1. 1. Map showing the studied area where the La Colonia Formation outcrops, Chubut Province, Patagonia, Argentina. 2. Sampled localities (red dots). 3. Schematic section of the La Colonia Formation exposed at the Plesiosaurio locality with indication of the fertile samples of salvinialean spores (arrows indicate the levels with megaspores). Lithological references: C: clay; S: silt; vf: very fine sandstone; f: fine sandstone; m: medium sandstone; c: coarse sandstone; vc: very coarse sandstone. 4. Outcrops of the studied area at the Plesiosaurio locality. 5. Typical gray mudstones of the La Colonia Formation. 6. Outcrop photo showing the Puntudo Chico – La Colonia formations boundary at the Chiva Muerta locality. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19

(Ardolino and Franchi, 1996; Anselmi et al., 2004; Sacomani et al., 2007). Biostratigraphic estimates (Malumián et al., 1991; Ardolino and Franchi, 1996; Page et al., 1999; Náñez and Malumián, 2008; Guler et al., 2014) and recent paleomagnetic analyses (W. Clyde pers. comm.) support a Maastrichtian to Danian age for the La Colonia deposits. All the studied samples in which megaspores were found are presumed to be of Maastrichtian age.

The La Colonia Fm. sections measured at the Mirasol Chico Creek area reaches (Fig. 1, 2) ~130 m thick. The lower part is characterized by a basal transgressive conglomerate followed by shoreface deposits of 5 to 10 m thick in the proximity of the Cerro Buitre area (Cúneo et al., 2014). Most of the La Colonia deposits consists of thick, clayey or silty beds (massive, laminated, or heterolithic) with sporadic fine-grained sand beds deposited in freshwater coastal environments and lagoons associated with coastal sand bars (Cúneo et al., 2013, 2014; Fig. 1, 3–5). At the Plesiosaurio locality section, the contact between the La Colonia and Cerro Bororó formations occurs at the 108 m level and is marked by a distinct red bed at the top of the La Colonia Fm. (Fig. 1, 4). However, the typical shoreface facies of the basal part of the La Colonia Formation and the contact with the underlying Puntudo Chico are not exposed. The contact between the Puntudo Chico and La Colonia formations are well exposed at the Chiva Muerta locality (Fig. 1, 6).

The La Colonia Fm. is characterized by its highly diverse and rich biota that comprises vertebrates (such as dinosaurs, plesiosaurs, turtles, mammals, birds, marine and freshwater fishes), invertebrates (e.g., bivalves, ostracods and foraminifera), and plants (including angiosperms, gymnosperms, and pteridophytes, and freshwater green algae). The presence of the freshwater green algae (*Botryococcus* Kützing, *Pediastrum* Meyen, and Zygnemataceae) together with water ferns and a species of the free-floating Araceae clade and *Nelumbo* Adamson indicates the occurrence of wetland (fresh water) communities at the time of deposition (Gandolfo et al., 2014; Cúneo et al., 2014; De Benedetti et al., 2018 and cites therein).

2.2. Fossil specimen sampling, preparation and curation

The studied specimens were obtained from samples collected at five localities: Cañadón del Irupé (CI), Quebrada del Helecho (QH), Cerro Bosta (CBO), Plesiosaurio (LCP), and Chiva Muerta (CHM) (Fig. 1, 1–2). At CI and QH, several palynological samples were collected from the level that yields the aquatic megafossil plants described in Cúneo et al. (2014). At CBO, 41 samples were collected along a 90 m section whereas 22 palynological samples were collected along a 108 m section at LCP. At CHM, 6 samples were collected from the lower 30 m of the formation, located above the continental sediments of the Puntudo Chico Fm. Stratigraphic sections of these localities have been previously illustrated in Cúneo et al. (2014) and De Benedetti et al. (2020). Here we illustrate the LCP locality section because it is the most comprehensive and where a new *Azolla* species was found (Fig. 1, 3–5).

The samples were processed using standard palynological techniques; residues were filtered with 150 μm sieves to separate megaspores, and 10 μm sieves for microspores. For light microscopy (LM) observations, the specimens were mounted on slides with glycerin jelly. For scanning electron microscopy (SEM) observations, the specimens were mounted directly on stubs using double-sided tape. Longitudinal and transverse sections were made using a razor blade. LM observations were made with a Nikon Eclipse 80i microscope coupled with a Nikon DS-L4 camera (Nikon Corp., Minato, Tokyo, Japan) at the Museo Paleontológico Egidio Feruglio (MEF), Chubut, Argentina. SEM observations were made with a Philips XL30 TMP SEM (Philips, Amsterdam, North Holland, Netherlands) at the Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; a JEOL JSM-6460 SEM (Jeol Ltd., Akishima, Tokyo, Japan) at Aluar S. A., Puerto Madryn, Chubut Province, Argentina, and a desktop Phenom XL SEM (Phenom-Worl B. V., Eindhoven, The Netherlands) at the L.H. Bailey Hortorium, Cornell University, Ithaca, New York, U.S. All images were edited using Adobe Photoshop CS6 (Adobe, San José, California, USA). Slides and SEM stubs containing the spores are housed at the palynological collection of the Museo Paleontológico Egidio Feruglio (MEF; repository acronyms MPEF-PA), Trelew, Chubut, Argentina.

2.3. Terminology

In this study, we applied the term "perine" for the outermost distinctlayer/s of the spore wall outside of the continuous exine as used by Collinson et al. (2013) and Schneider and Pryer (2002) for salviniaceous and marsileaceous spores. We used the term "acrolamella" for the proximal extension of the perine of all the modern and fossil genera related to the heterosporous water ferns, except for *Azolla*, for which the term "columella" is widely accepted by most of the authors (Fowler and Stennett-Willson, 1978; Van der Burgh et al., 2013; De Benedetti et al., 2018; among others). Terminology for *Azolla* megaspores follows Fowler and Stennett-Willson (1978). The term "infrafilosum" is used for referring the perinal hairs that originate below the collar region on the megaspore surface. The term "suprafilosum" has been applied for the proximal "superstructure of hairs" arising from the collar region and columella (e.g., Fowler and Stennett-Willson, 1978), but also occasionally for the perinal hairs that develop from the surface of the floats (e.g., Batten and Collinson, 2001; Van der Burgh et al., 2013; De Benedetti et al., 2018; among others). We used the term "apical mat" to differentiate the part of the suprafilosum that protrudes apically between the floats and covers them to a greater or lesser extent.

3. Results

A list of all samples in which the spores were recorded (with the acronyms and GPS data) is provided as supplementary material (Appendix). The identified species are described alphabetically within each family, and the species with uncertain family placement are at the end.

Order: Salviniales Link, 1833

Family: Marsileaceae Mirbel, 1802

Genus: **Crybelosporites** Dettmann, 1963

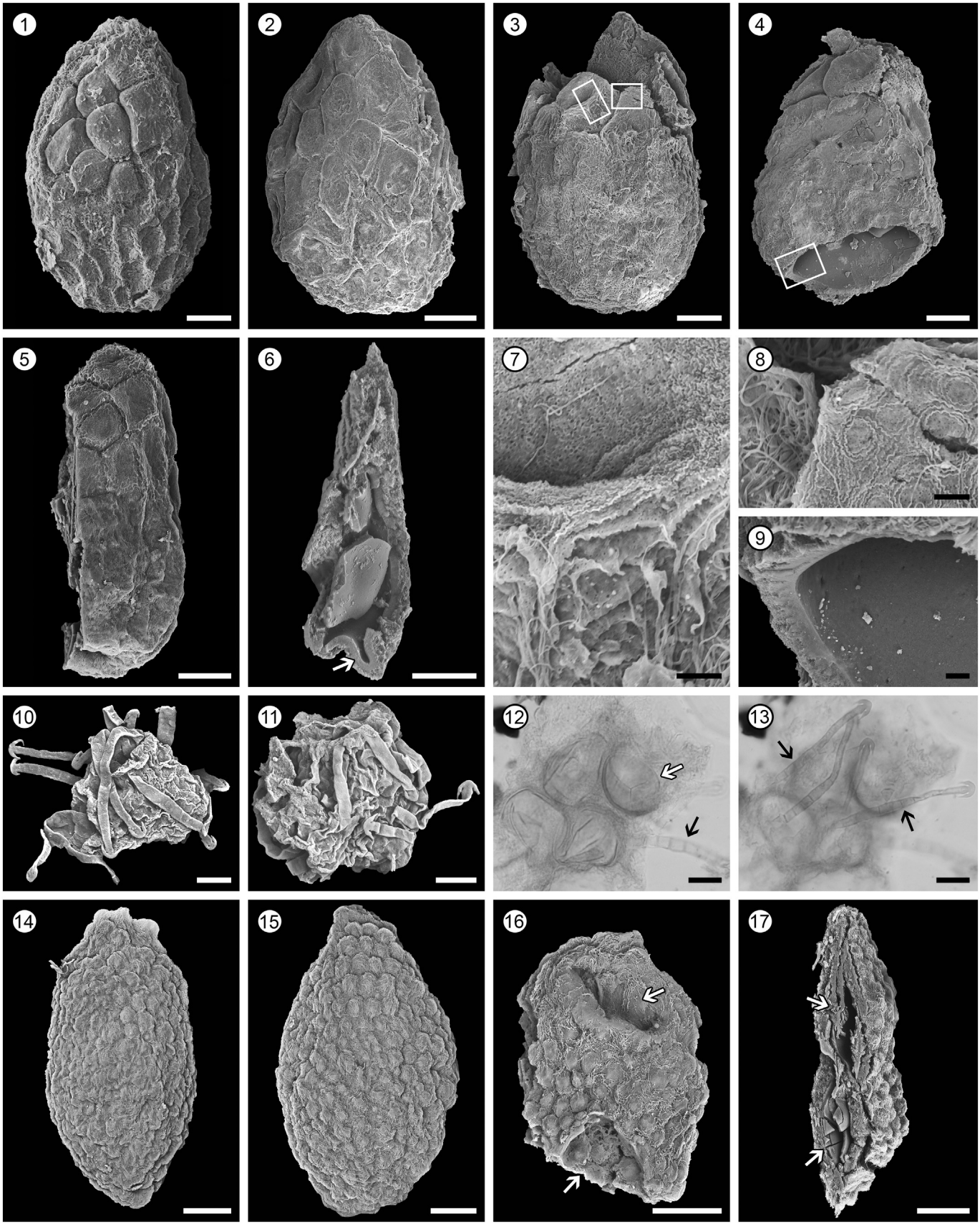
Type species: *Crybelosporites striatus* (Cookson and Dettmann, 1958) Dettmann, 1963

Crybelosporites pannuceus (Brenner, 1963) Srivastava, 1977

Plate I, 1–6

Description: Microspore spheroidal, with a trilete mark about three-quarter of the spore radius and obscured by an acrolamella (sometimes apparently absent). Microspore wall 5–8 μm thick composed of an inner exine and an outer perine. Exine 1.0–2.0 μm thick, psilate. Perine two-layered; inner perine 0.5–1.0 μm thick, granular; outer perine 3–6 μm thick, strongly rugulate-reticulate, with anastomosed folds forming irregular lumina of 2.3–5.5 μm diameter.

Plate I. 1–6. *Crybelosporites pannuceus*. 1–4. Specimens with robust folds. 1. Specimen at SEM in lateral view. 2. Specimen at SEM in proximal view, the acrolamella has been lost revealing the trilete mark. 3,4. Specimens at LM. 5,6. Specimens with thinner folds. 1. MPEF-PA 150. 2. MPEF-PA 151. 3. MPEF-PA 752. 4. MPEF-PA 753. 5,6. MPEF-PA 149. 7–13. *Gabonisporis cristata*. 7. Specimen at SEM. 8. Detail of 7. Note the microreticulate flared outer-edge of the goblet-shaped elements. 9. Transversal section showing the goblet-shaped elements. 10–13. Specimens at LM (10 and 11: same specimen at different optical view). 7,8. MPEF-PA 149. 9. MPEF-PA 171. 10,11. MPEF-PA 581. 12. MPEF-PA 580. 13. MPEF-PA 752. 14,16,17. *Molaspora lobata*. 14. Specimen at SEM. 16. Detail of the baculate surface. 17. Transversal section showing the megaspore wall. 14. MPEF-PA 210; 16. MPEF-PA 105; 17. MPEF-PA 101. 15,18,19. *Molaspora reticulata*. 15. Specimen at SEM. 18. Transversal section showing the megaspore wall. 19. Detail of the reticulate surface. 15,19. MPEF-PA 208. 18. MPEF-PA 207. Scale bars: 1–7,10–13 = 10 μm; 8 = 3 μm; 9 = 2 μm; 14 = 100 μm; 15 = 40 μm; 16–19 = 5 μm.


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17

Dimensions: Equatorial diameter 26 (43) 71 μm; length of acrolamella 4–11 μm; width of acrolamella 9–22 μm (64 specimens measured).

Studied material: MPEF-PA 149–151, 450–454, 581, 582, 585, 587, 614, 621–625, 751–753, and 781.

Remarks and comparisons: There are some morphological variations in the specimens recorded in the La Colonia. Most of them have a well-developed acrolamella and a strongly rugulate surface with robust folds (Plate I, 1–4), while others apparently lack of an acrolamella and have thinner folds forming a more reticulate sculpture (Plate I, 5, 6). The specimens described here have a wider size range (26–71 μm diameter) than that given in the species diagnosis (36–59 μm diameter) by Brenner (1963).

Previous record: *C. pannuceus* has been widely recorded worldwide exclusively in Cretaceous deposits (Brenner, 1963, 1968; Herngreen, 1973; Kotova, 1978; Salard-Cheboldaeff, 1990; Lupia et al., 2000; Ibrahim et al., 2001; Villanueva-Amadoz et al., 2011; Cúneo et al., 2013, 2014; Hermsen et al., 2013; Puebla et al., 2014; Li et al., 2019; among others).

Genus: **Gabonisporis** Boltenhagen, 1967 emend. Srivastava, 1972

Type species: *Gabonisporis vigourouxii* Boltenhagen, 1967

Gabonisporis cristata (Stanley, 1965) Sweet, 1986

Plate I, 7–13

Description: Microspore spheroidal, with a trilete mark reaching the equator. Microspore wall 4–8 μm thick composed of an inner exine and an outer perine. Exine 1.0–1.5 μm thick, psilate. Perine 3–7 μm thick composed of elongated goblet-shaped elements, 1.5–3.0 μm in diameter on surface and 0.5–0.6 μm in diameter at bases. Goblet-shaped elements with flared outer edge somewhat upturned, lobed, 1.0–1.2 μm wide, microreticulate, lumina ~0.2–1.0 wide, muri ~0.2–0.5 μm wide.

Dimensions: Equatorial diameter 26 (42) 66 μm (26 specimens measured).

Studied material: MPEF-PA 149, 171, 576, 580, 581, 585, 586, 622–624, 692, 693, 750, 751, 803, and 847.

Remarks and comparisons: The Patagonian specimens are closely similar to those described by Srivastava (1972) as *Gabonisporis bacaricumulus* from the Maastrichtian of Canada, later considered a synonym of *G. cristata* by Sweet (1986). The La Colonia specimens are characterized by having a microreticulate surface on the outer-rim of the goblet-shaped elements, which is punctate in the Canadian specimens (Srivastava, 1972). The specimens described here have a wider size range (26–66 μm diameter) than that given in the species diagnosis (40–55 μm diameter) by Stanley (1965) and Srivastava (1972).

This is the first report of *G. cristata* for South America and the Southern Hemisphere.

Previous record: G. cristata has been widely recorded in Campanian to Eocene deposits in the Northern Hemisphere (Rouse, 1962; Stanley, 1965; Srivastava, 1972; Sweet, 1986; Yi and Batten, 2002; Rai and Sharma, 2004; Mahmoud and Schrank, 2007; Samant et al., 2008; Aulenback, 2009; Srivastava and Braman, 2013; Braman, 2018; Peyrot et al., 2019; among others).

Genus: **Molaspora** Schemel, 1950 emend. Hall, 1963

Type species: *Molaspora lobata* (Dijkstra, 1949) Hall, in Hall and Peake, 1968.

Molaspora lobata (Dijkstra, 1949) Hall, in Hall and Peake, 1968.

Plate I, 14, 16, 17.

Description: Megaspore subspherical, with a prominent acrolamella composed of five to seven small, leaf-like lobes which are usually twisted to form a short cone. Megaspore wall 15–21 μm thick composed of an inner exine and an outer perine. Exine 2.0–3.0 μm thick, psilate. Perine two-layered; inner perine 1.0–1.5 μm thick, granular; outer perine 13–18 μm thick, alveolate grading into hollow baculate-papillate to clavate elements.

Dimensions: Maximum diameter of megaspore 315 (390) 520 μm (14 specimens measured); length of acrolamella 53 (88) 144 μm, width of acrolamella 100 (130) 162 μm (6 specimens measured).

Studied material: MPEF-PA 87, 101, 105, 210, and 211.

Previous record: M. lobata has been widely recorded in Cretaceous deposits worldwide (Hall, 1963; Hall and Peake, 1968; Batten, 1987; Lupia et al., 2000; Takahashi et al., 2001; Batten et al., 2011a, 2011b; Lupia, 2011; Cúneo et al., 2013; Vallati et al., 2017; Zavialova and Batten, 2018; among others).

Molaspora reticulata Campbell and Untergasser, 1972

Plate I, 15, 18, 19

Description: Megaspore subspherical, with a prominent acrolamella composed of five to seven small, leaf-like lobes which are usually twisted to form a short cone. Megaspore wall 15–21 μm thick, composed of an inner exine and an outer perine. Exine psilate, 2.5–3.0 μm thick. Perine two-layered; inner perine granular, 1.0–1.5 μm thick; outer perine 8.5–14.0 μm thick, alveolate and grading into delicate membranes that forms a perfect reticulum with lumina of 2.5–9.0 μm diameter.

Dimensions: Maximum diameter of megaspore 163 (222) 274 μm (5 specimens measured); length of acrolamella 43 (70) 91 μm, width of acrolamella 56 (94) 138 μm (4 specimens measured).

Studied material: MPEF-PA 106, 206, 207, and 208.

Remarks and comparisons: M. reticulata was first described from the Campanian–Maastrichtian of Canada (Campbell and Untergasser, 1972). The Canadian specimens differ in the larger size (244–398 μm diameter), the thicker perine (up to 33 μm thick), and the reticulum with slightly wider lumina (10–15 μm diameter). This constitutes the first report of *M. reticulata* for South America and the Southern Hemisphere.

Previous record: Late Cretaceous of North America (Campbell and Untergasser, 1972; Aulenback, 2009; Kutluk and Hills, 2015).

Family: Salviniaceae Martinov, 1820

Genus: **Azolla** Lamarck, 1783

Type species: *Azolla filiculoides* Lamarck, 1783

Azolla andreisii De Benedetti and Zamaloa sp. nov.

Plate II, 1–9

Etymology: The specific epithet honors the late Dr. Renato R. Andreis, prominent Argentine geologist, who was the first to describe the stratigraphic section at the Plesiosaurio locality.

Type locality: Plesiosaurio locality, La Colonia Formation, Chubut Province, Argentina.

Other localities: Cerro Bosta locality, La Colonia Fm., Chubut Province, Argentina.

Holotype: MPEF-PA 207 (Plate II, 1).

Paratypes: MPEF-PA 204, 207 (Plate II, 2–6).

Repository: Palynological Collection at the Museo Paleontológico Egidio Feruglio (MPEF-PA), Trelew, Chubut Province, Argentina.

Stratigraphic horizon: La Colonia Formation, Late Cretaceous (Maastrichtian).

Plate II. 1–9. *Azolla andreisii* n. sp. 1. Megaspore apparatus with five poorly defined levels of floats (holotype). 2. Specimen with rhombic floats of regular size, most of them with a central invagination. 3. Fragmented specimen. 4. Specimen sectioned at the megaspore level. 5,6. Longitudinal sections. Note the thickness of the exine relative to the perine in 6 (*arrow*). 7. Detail of an invaginated float showing the outer (top) and inner (bottom) surface. Note the rugulate outer surface at the upper part, and the perinal hairs arising from the inner surface at the lower part (detail of 3). 8. Float with rugulate surface and fused wrinkles defining a concentric wavy pattern (detail of 3). 9. Close up of megaspore wall. Note the smooth inner surface of the exine (detail of 4). 1–4,7–9. MPEF-PA 207. 5,6. MPEF-PA 204. 10–13. *Azolla* sp. 1. 10,11. Specimens at SEM. Note the anchor-shaped glochidia with broad stalk. 12,13. Same specimen at LM in different optical view. Note the four trilete microspores (*white arrow*) in 12, and the septate glochidia (*black arrows*) in 12 and 13. 10,11. MPEF-PA 165. 12,13. MPEF-PA 929. 14–17. *Azollopsis intermedia*. 14–16. Megaspore apparatus with numerous circular floats enmeshed in perinal hairs and covering the entire surface. Note the two megaspore cavities in 16 (*arrows*). 17. Specimen longitudinally sectioned showing two megaspores (*arrows*). 14–16 MPEF-PA 104. 17 MPEF-PA 204. Scale bars: 1–6,14–17 = 100 μm; 7–9,10–13 = 10 μm.

Table 1
Main characteristics of the megaspore apparatus of *Azolla* multifloated species.

Azolla species	Total length	Filosum	Megaspore surface	Collar	Apical mat	Float number/ distribution	Float size/Morphology	Float surface	Age/Distribution	Bibliography
Azolla andreisii	588–700 μm	Scarce on floats, dense on megaspore	Obscured by hairs	Absent	Absent	>20 / three to five irregular tiers	87–155 μm / rhombic, subrectangular, polygonal or irregular	Rough or wrinkled	Maastrichtian / Chubut, Argentina	*This paper*
Azolla anglica	446–599 μm	Dense on floats, scarce on megaspore	Foveolate/reticulate	Absent	Present	24 / three tiers	?	Obscured by hairs	Upper Paleocene / Kent, United Kingdom	(Martin, 1976a); Collinson et al. (2013)
Azolla arctica	350–400 μm	Dense on floats and megaspore	Rugulate, perforate	Present	Present	15–18 / three tiers	? / discoidal to spherical	Obscured by hairs	Eocene / Canada, near Arctic Ocean; Norwegian, Greenland Sea	Collinson et al. (2009, 2013)
Azolla areolata	346–595 μm	Dense on floats, scarce on megaspore	Foveolate (occasionally with exoperinal prolongations)	Absent	Present	18 (24) 27 / three tiers	85–212 μm / rhombic, subrectangular to polygonal	Obscured by hairs	Paleocene –?Eocene / Northwest Territories, Canada	Sweet and Hills (1976)
Azolla barbata	399–608 μm	Scarce on floats and megaspore	Foveolate	Absent	Absent	Numerous / two or more irregular tiers	? / spherical to polygonal	Smooth	Maastrichtian / Alberta, Canada; Montana-North Dakota, USA	Snead (1969); Hall and Bergad (1971)
Azolla boliviensis	380–400 μm	Scarce on floats and megaspore	Reticulate	Absent	Absent	30 / three tiers or spirals	10–25 μm / circular to subcircular	Smooth	Maastrichtian / Bolivia	Vajda and McLoughlin (2005)
Azolla bulbosa	385–555 μm	Dense on floats, scarce on megaspore	Irregularly reticulate (with exoperinal prolongations)	Absent	Present	21(24)27 / three tiers	95–180 μm / rhombic, subrectangular to polygonal	Obscured by hairs	Paleocene / Alberta, Canada	Snead (1969); Sweet and Hills (1976)
Azolla coloniensis	360–520 μm	Dense on floats and megaspore	Reticulate	Absent	Absent	18, 24, or more / three to four tiers	50–150 μm / rhombic, subrectangular, polygonal to elliptical	Reticulate-perforate	Maastrichtian / Chubut, Argentina	De Benedetti et al. (2018); Hermsen et al. (2019)
Azolla colwellensis	377–550 μm	Scarce on floats, dense on megaspore	Rugulate	Present	Present	18–24 / three tiers	? / quadrangular-hexagonal	Obscured by hairs	Eocene / United Kingdom	Collinson (1980)
Azolla conspicua	800–1000 μm	Dense on floats and megaspore	?	Absent	?	Numerous /?	? / Subrectangular	Obscured by hairs	Santonian – Maastrichtian / Alberta, Canada	Snead (1969); (Gunther and Hills, 1972)
Azolla distincta	470–630 μm	Dense on floats and megaspore	Reticulate	Absent	Present	Numerous / two tiers	? / discoidal	Obscured by hairs	Campanian – Paleocene / Alberta, Canada; South Dakota, USA	Snead (1969); Jain (1971); Hall and Bergad (1971);
Azolla filosa	500–525 μm	Dense on floats and megaspore	?	Absent	?	Numerous /?	?	Obscured by hairs	Maastrichtian / Alberta, Canada	Snead (1969); (Gunther and Hills, 1972)
Azolla lauta	560–640 μm	Dense on floats and megaspore	Rugulo-reticulate	Absent	Present	Numerous /?	?	Obscured by hairs	Maastrichtian – Paleocene / Alberta, Canada	Snead (1969); (Gunther and Hills, 1972)
Azolla montana	390–530 μm	Dense on floats and megaspore	Rugulo-reticulate	Absent	Present	10–20 / two tiers	Subcircular to polygonal	Obscured by hairs	Maastrichtian – Eocene / Montana and North Dakota, USA	(Hall and Swanson, 1968); Jain and Hall (1969); Hall (1974)
Azolla nuda	310–440 μm	Dense on floats and megaspore	Rugulate with small papillae	Present	Present	9 or 18 / two or three tiers	?	Obscured by hairs	Eocene / Norwegian, Greenland Sea	Van der Burgh et al. (2013)
Azolla primaeva	330–460 μm	Dense on floats, scarce on megaspore	Foveolate-reticulate	Present	Absent	11–20 / two or more tiers	10–65 μm / polygonal to irregular	Obscured by hairs	Maastrichtian – Eocene / Alberta, Canada	Arnold (1955); (Hills and Weiner, 1965); Collinson et al. (2017)
Azolla schopfii	340–600 μm	Scarce on floats and megaspore	Verrucate-clavate	Absent	Absent	15–22 / three tiers	35–140 μm / subcircular, subrectangular, subtriangular	Smooth to punctate	Maastrichtian – Paleocene / Alberta, Canada; South Dakota, USA	Sweet and Chandrasekharam (1973); McIver and Basinger (1993); Batten and Collinson (2001)
Azolla stanleyi	350–640 μm	Dense on floats and megaspore	Rugulo-reticulate	Absent	Present	15–24 / two or three tiers	105–185 μm / spherical, ovoid, conical, subrectangular	Obscured by hairs	Paleocene / Alberta and Saskatchewan, Canada; North Dakota, USA	Jain and Hall (1969); (Melchior and Hall, 1983); (Hoffman and Stockey, 1994)
Azolla teschiana	330–590 μm	Dense on floats, scarce on megaspore	Warty (with wart-like excrescences)	Absent	Absent	24 / three tiers	70–120 μm / rounded	Obscured by hairs	Paleocene –?Eocene / Netherland, Belgium, Germany, United Kingdom	(Hills and Gopal, 1967); (Kempf, 1969); Batten and Collinson (2001)
Azolla velus	350–570 μm	Dense on floats and megaspore	Reticulate	Absent	Present	Numerous?	?	Obscured by hairs	Paleocene / South Dakota and Montana, USA; Saskatchewan, Canada	(Martin, 1976b); McIver and Basinger (1993); Batten and Collinson (2001)

Diagnosis: Megaspore apparatus oval to elliptical, with a spherical to subspherical megaspore and a proximal float apparatus. Megaspore surface completely covered by a thick mat of intertwined hairs. Float apparatus composed of more than 20 pseudovacuolate floats arranged in three to five poorly defined tiers. Floats spherical, elliptical, quadrangular, rhombic, or irregular in shape and with a rough or wrinkled surface. Vegetative remains and microspore massulae unknown.

Description: Megaspore apparatus oval to elliptical, composed of a spherical to subspherical megaspore and a float apparatus situated proximally (Plate II, 1–5). Megaspore wall composed of a homogeneous exine of 8–12 μm thick and a granular to spongy perine of 5–20 μm thick from which a dense mat of perinal hairs extends (infrafilosum) (Plate II, 4, 6, 9). The perinal hairs are c. 0.5–2.0 μm thick and cover completely the megaspore surface. The differentiation between endo- and exoperine is obscure. The float apparatus is composed of more than 20 pseudovacuolate floats that are arranged in three to five poorly defined tiers (Plate II, 1–5). The floats are of variable shape (commonly rhombic, possibly as a consequence of preservational processes), and very variable in size (87–155 μm). The upper level comprises probably only three floats, while the lower level is usually the most numerous and with smaller floats which cover part of the megaspore body. Some specimens possess only rhombic floats of regular size in all the tiers, most of them with a central invagination (Plate II, 2). The floats have a rough surface, sometimes with fused wrinkles defining a concentric wavy pattern (Plate II, 7, 8). Additional puncta can also be present on the float surface of some specimens. The inner surface of the floats develops numerous extensions that narrow distally to form long perinal hairs (suprafilosum) (Plate II, 7).

Dimensions: Length of megaspore apparatus 588 (657) 700 μm, width of megaspore apparatus 306 (400) 455 μm (5 specimens measured); diameter of megaspore 328 μm (one specimen measured); diameter of floats 87 (121) 155 μm (25 specimens measured).

Remarks and comparisons: Currently there are 20 multifloated *Azolla* species recognized in the fossil record from the Santonian–Maastrichtian to the Eocene, including *A. andreisii*. The main characteristics of the megaspore apparatus of these species are summarized in Table 1.

All *Azolla* multifloated species, including the new species *A. andreisii*, have more than nine floats arranged in two or more tiers on the proximal pole of the megaspore apparatus. *A. andreisii* can be easily distinguished from *A. anglica* Martin, 1976a, *A. arctica* Collinson et al., 2009, *A. areolata* Sweet and Hills, 1976, *A. bulbosa* Snead, 1969, *A. colwellensis* Collinson, 1980, *A. distincta* Snead, 1969, *A. lauta* Snead, 1969, *A. montana* Hall in Hall and Swanson 1968 emend. Jain and Hall, 1969, *A. nuda* Van der Burgh et al., 2013, *A. stanleyi* Jain and Hall, 1969, and *A. velus* (Dijkstra, 1961) Jain and Hall, 1969 emend. Batten and Collinson, 2001, due to the presence of an apical mat of hairs that protrudes between the floats and covers them to a lesser or greater extent. This apical mat is sometimes accompanied by a persistent apical cap ("apical membrane" of Fowler and Stennett-Willson, 1978) attached to the apical hairs, as occurs in *A. anglica*, *A. arctica*, *A. colwellensis*, and *A. nuda*. In *A. andreisii*, perinal hairs arise from the inner surface of the floats and become entangled with those of the central columella but they do not protrude apically between the floats covering them. Furthermore, in *A. anglica*, *A. areolata*, and *A. bulbosa* the filosum is scarce on the megaspore surface that, is additionally ornamented by exoperinal prolongations in the last two species (Collinson et al., 2013; Martin, 1976a; Snead, 1969; Sweet and Hills, 1976). *A. arctica*, *A. colwellensis*, and *A. nuda* can also be distinguished from *A. andreisii* by the presence of a collar (Collinson, 1980; Collinson et al., 2009, 2013; Van der Burgh et al., 2013).

A. barbata Snead, 1969 and *A. boliviensis* Vajda and McLoughlin, 2005 are different from *A. andreisii* by having a scarce filosum over the megaspore surface and by the smooth subcircular to polygonal floats (Hall and Bergad, 1971; Vajda and McLoughlin, 2005). Additionally, the floats are very small (up to 25 μm diameter) in *A. boliviensis* in comparison with those of *A. andreisii* (up to 155 μm diameter). Unfortunately, the descriptions of *A. conspicua* Snead, 1969 and *A. filosa* Snead, 1969 are meager, but they are clearly distinctive from *A. andreisii* by having a dense filosum on the floats. Moreover, *A. conspicua* is larger (800–1000 μm) than *A. andreisii* (588–700 μm) while *A. filosa* is smaller (500–525 μm).

A. primaeva (Penhallow, 1908) Arnold, 1955 emend. Collinson et al., 2017, is doubtfully included here among the multifloated species. According to Collinson et al. (2017, p. 22): "If the pale patches with darker boundaries were considered to be floats, then *A. primaeva* would be a multifloated species with very variable float number and a very poorly organized float zone." The floats of *A. primaeva* are completely covered by hairs and have a granular structure, which differs from all previously known modern and fossil species whose floats are pseudovacuolated (Collinson et al., 2017).

The megaspore surface of *A. schopfii* Dijkstra, 1961 emend. Batten and Collinson, 2001 is practically devoid of filosum and the floats are subcircular, subrectangular to subtriangular but never rhombic, and their surface is smooth to punctate (Snead, 1969; Sweet and Chandrasekharam, 1973; McIver and Basinger, 1993; Batten and Collinson, 2001). *A. teschiana* Florschütz, 1945 emend. Batten and Collinson, 2001 is easily distinguished from *A. andreisii* by the presence of wart-like excrescences on the megaspore surface and floats mostly covered by hairs.

Among the Patagonian species, *A. coloniensis* De Benedetti and Zamaloa 2018 emend. Hermsen et al., 2019 has reticulate-perforate floats that are usually covered by hairs and the megaspore apparatuses are notably smaller (up to 520 μm) than those of *A. andreisii* (up to 700 μm). *A. colhuehuapensis* Vallati et al., 2017 is easily distinguished from the new species as it has nine floats in two tiers. *A. keuja* Jud et al. in Hermsen et al., 2019 has apparently six floats in a single tier that are obscured by an apical cap and the megaspore surface possess large excrescences.

The float surface of most multifloated *Azolla* species is covered by hairs and its surface ornamentation is therefore unknown. In the few species for which the float surface has been described it is smooth to punctate (*A. barbata*, *A. boliviensis*, and *A. schopfii*) or reticulate-perforate (*A. coloniensis*). The presence of strongly invaginated floats is only known in two of the La Colonia species: *A. andreisii* and *A. coloniensis*. All known multifloated species have floats arranged in two or three tiers while there are up to five irregular tiers in *A. andreisii*.

In sum, the floats with a rough surface arranged in up to five irregular tiers, and occasionally invaginated distinguish *A. andreisii* from the other known multifloated *Azolla* species.

Azolla coloniensis De Benedetti and Zamaloa 2018 emend. Hermsen, Jud and Gandolfo 2019

Description: see De Benedetti et al. (2018) for a detailed description.

Studied material: MPEF-PA 80–99, 204, 209–211, 580–582, 585, and 623.

Remarks and comparisons: A. coloniensis was initially described by De Benedetti et al. (2018) based on mega- and microspores, and later emended by Hermsen et al. (2019) to include sporophytes in organic connection with the reproductive structures.

Previous record: This species is only known from the Maastrichtian of the La Colonia Fm., Chubut Province, Argentina (De Benedetti et al., 2018; Hermsen et al., 2019).

Azolla sp. 1

Plate II, 10–13

Description: Microspore massulae oval to irregular in outline, pseudovacuolate in structure, and containing 3 to 4 spheroidal trilete microspores. Microspore exine psilate, with the laesurae extending one third the diameter of the spore. Surface of the massula faintly granulated and with numerous anchor-shaped glochidia of up to 68 μm long, and with numerous septa delimiting glochidial cells. The glochidia have a broad stalk that narrows distally, a distal dilation and a constriction beneath the anchor-shaped tips. The hooks are mostly recurved.

Dimensions: Maximum length of microspore massulae 40 (73) 147 μm (7 specimens measured); diameter of microspore 17 (23) 29 μm (11 specimens measured); length of glochidium 45–68 μm, width of glochidium 2.5–5.5 μm; length of glochidium cell 2–5 μm.

Studied material: MPEF-PA 165, 611, 623–625, 929, 956, 989, and 993.

Remarks and comparisons: Microspore massulae of *Azolla* sp. 1 were found constantly associated with the megaspores of *A. andreisii*. However, both spores are described separately because no massulae were found attached to the megaspores.

Microspore massulae of *A. coloniensis* also have anchor-shaped glochidia, but they are aseptate and smaller (~ 30 μm long and 1.2–1.7 μm wide; De Benedetti et al., 2018). Microspore massulae similar to *Azolla* sp. 1 were recorded at the Maastrichtian Lago Colhué Huapi Formation approximately 200 km south of the La Colonia Fm. (fig. 4.13 in Vallati et al., 2016; '*Azolla* sp. 2' fig. 4.J–L in Vallati et al., 2017).

Family: Incertae sedis

Genus: **Azollopsis** Hall, 1968 emend. De Benedetti and Zamaloa.

Type species: *Azollopsis coccoides* Hall, 1968 emend. Sweet and Hills, 1974

Original generic diagnosis (in Hall, 1968, p. 81): "Megaspore apparatus with a conspicuous, tomentose perispore and a spherical, trilete endospore. Numerous float-like structures imbedded in or attached to the hairs of the perispore. Massulae with few microspores and conspicuous multi-hooked or barbed glochidia. Vegetative remains unknown."

Emended generic diagnosis (in Sweet and Hills, 1974, p. 1628): "Megaspore complexes usually composed of floats, perine, and megaspore. Floats usually numerous, circular, embedded in filosum, attached by filament entanglement, and regularly distributed over entire surface of megaspore complex. Float position reflected in perinal layers by corresponding subcircular indentations. Inperine extended into proximal trifolium-like appendage. Intertrifolium areas infilled by expansion of exoperine and filosum. Massulae usually with a few large microspores and multibarbed or circinate glochidia. Vegetative remains unknown."

Emended generic diagnosis (this paper): Megaspore apparatus composed of floats, perine, and one or two trilete megaspores. Floats numerous, circular to elliptic, embedded in filosum, attached by filament entanglement, and regularly distributed over the entire surface of the megaspore apparatus. Float position reflected in perinal layers by corresponding subcircular indentations. Massulae usually with a few large microspores and multibarbed or circinate glochidia. Vegetative remains unknown.

Comments: Azollopsis is emended here to include megaspore apparatuses containing more than one megaspore. Furthermore, the presence of a "trifolium-like appendage" (acrolamella) was excluded from the diagnosis because it is not present when the megaspore apparatus comprises two megaspores.

Azollopsis differs from *Paleoazolla* due to the presence of floats, which, if present in *Paleoazolla*, they are embedded in the vacuolated perine.

Azollopsis intermedia Sweet and Hills, 1974.

Plate II, 14–17; Plate III, 1–12.

Description: Megaspore apparatus elliptic to ovate, containing one or two spherical trilete megaspores (Plate II, 14–17). Megaspore exine 3–6 μm thick (Plate III, 2). A dense mat of intertwined hairs and more than 200 circular to ovoid floats develop from a common spongy perine that surrounds the megaspores. Floats attached by filament entanglement and regularly distributed over the entire surface (Plate II, 14–17; Plate III, 1). Microsporangium ovate, containing seven or more microspore massulae (Plate III, 3, 4) which are subcircular, ovate, subrectangular to irregular in outline, pseudovacuolate in structure and with conspicuous circinate aseptate glochidia (Plate III, 5–7, 10–12). Numerous glochidia are commonly present in the inner surface and the contact area between the massulae in a microsporangium, while the outer surface is psilate to locally granular and mostly devoid of glochidia (Plate III, 5). Massulae contain about 8–12 trilete microspores (Plate III, 10–12), the laesurae occupies all the diameter of the spore (Plate III, 8). Microspore exine microgranular, 1 μm thick (Plate III, 9).

Dimensions: Length of megaspore apparatus 498 (615) 694 μm, width of megaspore apparatus 268 (312) 393 μm (7 specimens measured); diameter of megaspore 190 (238) 282 μm (4 specimens measured); diameter of floats 19 (39) 58 μm (44 floats measured); thick of perinal hairs 0.5–2.0 μm; length of microsporangia groups 346 (416) 507 μm (3 specimens measured); maximum length of microsporangium 164 (234) 356 μm (14 specimens measured); maximum length of microspore massulae 67 (140) 192 μm (21 specimens measured); diameter of microspore 22 (29) 38 μm (39 specimens measured); length of glochidium 6–116 μm, width of glochidium 0.5–3.5 μm.

Studied material: MPEF-PA 104, 204, 206, 306, 311, 312, 317, and 612.

Remarks and comparisons: Megaspores of *A. intermedia* were found always in association with their microspore massulae but not attached. According to Sweet and Hills (1974) there are more than 256 floats and 1 to 7 microspores per massulae in *A. intermedia*. In the La Colonia specimens, the number of floats could not be exactly determined but they are definitely more than 200, and there are about 8–12 microspores per massulae. The megaspore apparatuses of *A. intermedia* in the Patagonian populations are closely similar to those described for the Late Cretaceous of North America; the major difference is the presence of two megaspores in some Patagonian megasporangia. The development of two megaspores per megasporangium is characteristic of *Paleoazolla patagonica*. In this way, there is a notable similarity between the megaspore apparatus of *Azollopsis intermedia* and *P. patagonica*, which mainly differ on the presence of well-developed floats in the former while in *Paleoazolla*, when floats are present, they are embedded in the outer perine.

This constitutes the first record of *A. intermedia* megaspores for South America and the Southern Hemisphere.

Previous record: A. intermedia was first described from the Late Cretaceous of North America (Sweet and Hills, 1974; Speelman and Hills, 1980). Isolated megaspores were also reported from the Coniacian-Campanian of Hungary (Rákosi and Barbacka, 2000), while dispersed microspore massulae were reported from the Paleocene of Argentina (Volkheimer et al., 2007; Scafati et al., 2009).

Azollopsis tomentosa Hall, 1968

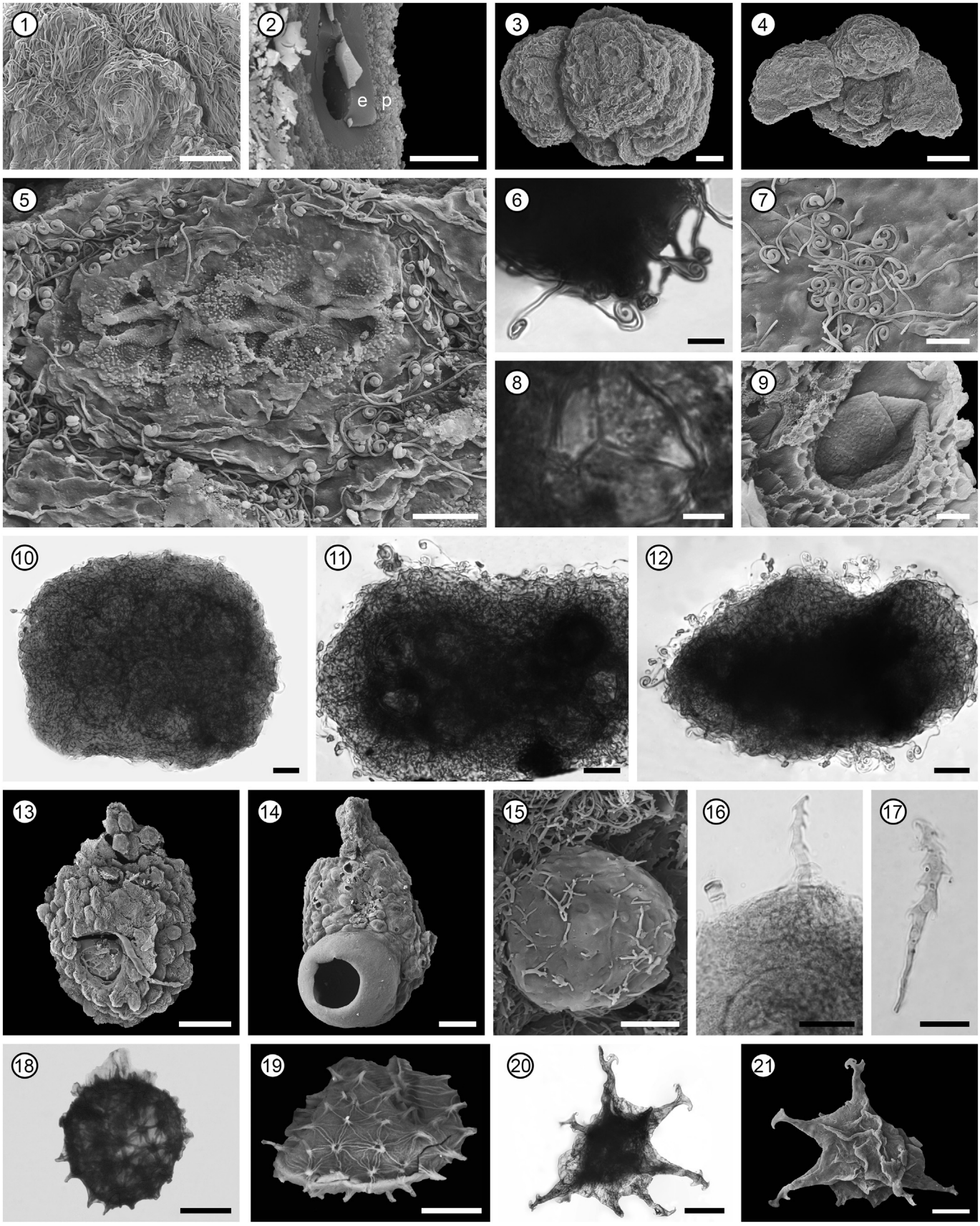
Plate III, 13–17

Description: Megaspore apparatus subspheroidal to ovate containing one spherical megaspore covered by a dense mat of intertwined hairs and numerous circular to ovoid floats (Plate III, 13, 14). Floats attached by filament entanglement and regularly distributed over the entire surface (Plate III, 15). Microspore massulae subcircular to ovate in outline with conspicuous septate multibarbed glochidia and containing few large microspores (Plate III, 16, 17). Glochidia with opposite or alternate barbs and double to single-barbed tips (Plate III, 16, 17).

Dimensions: Length of megaspore apparatus 440 μm, width of megaspore apparatus 318 μm (one specimen measured); diameter of floats 31 (39) 44 μm (13 floats measured); thick of perinal hairs 0.5–2.0 μm. Maximum length of microspore massulae ~200 μm (one specimen measured); diameter of microspore ~40 μm (2 specimens measured); thick of exine 1 μm; length of glochidium 40–42 μm, width of glochidium 3.0–3.5 μm (thinned toward the base).

Studied material: MPEF-PA 104, 201, 651, and 693.

Remarks and comparisons: Despite the large number of megaspores recovered from the different levels of the La Colonia Fm., only a few specimens can be undoubtedly assigned to this species. *A. tomentosa* possess 130 to 225 floats in the megaspore apparatus and 1 to 8 microspores per massulae (Sweet and Hills, 1974). Although the number of floats in the La Colonia specimens could not be determined they are clearly numerous. The microspore massulae are rare and poorly


1
2
e p
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21

preserved and the number of microspores per massulae is hard to determine.

According to Hall, 1968 and Sweet and Hills (1974), *A. tomentosa* represents an evolved species of *A. coccoides*, and the assignment of megaspores to one or the other species is difficult because their characters sometimes overlap. The megaspore apparatus of *A. tomentosa* illustrated here (Plate III, 13) is very similar to that described as *A. coccoides* by Sweet and Hills (pl. III, 13 in Sweet and Hills, 1974). However, the massulae of *A. coccoides* are smaller, have fewer microspores, and the glochidia are more frequently distinctly septate, oppositely barbed, and have tips which tend to be double-barbed (Sweet and Hills, 1974, p. 1630). In the Patagonian material (Plate III, 16, 17) the glochidia are like those of *A. tomentosa* (— figs 9 and 14 in Hall, 1968) with mostly alternate barbs and single-barbed tips. Sweet and Hills (1974, p. 1634) also suggested that differences between both species could be the result of geographical factors rather than evolutionary change.

This constitutes the first record of *A. tomentosa* megaspores from South America and the Southern Hemisphere.

Previous record: A. tomentosa was originally described from the Late Cretaceous of North America (Hall, 1968; Jain, 1971; Srivastava, 1968; Sweet and Hills, 1974). Isolated microspore massulae of this species were later reported from the Late Cretaceous of India (Venkatachala and Sharma, 1974; Nandi and Chattopadhyay, 2003) and the Late Cretaceous and Paleocene of Argentina (Volkheimer et al., 2007; Scafati et al., 2009; Barreda et al., 2012). Megaspores of *A. tomentosa* were also reported from the Late Cretaceous of Hungary (Rákosi and Barbacka, 2000).

Genus: **Ghoshispora** Srivastava, 1967 emend. Dettmann, 1995

Type species: *Ghoshispora scollardiana* Srivastava, 1967 emend. Srivastava, 1978

Ghoshispora sp.

Plate III, 18, 19.

Description: Megaspore with a small membranous triradiate proximal acrolamella. Spore body sculptured with ribbed processes connected by muri 1 μm wide and 1–2 μm high forming a reticulum with triangular lumina. Additional ribs within the triangular lumina are slightly lower and connected by tinny muri forming a poorly defined secondary microreticulate pattern. All ribs converge toward and extend onto the basal part of the processes.

Dimensions: Total length 140 (164) 200 μm (3 specimens measured); megaspore diameter 140 μm (1 specimen measured); length of acrolamella 38 μm, width of acrolamella 100 μm (1 specimen measured); length of processes 14–22 μm; distance between processes 14–29 μm.

Studied material: MPEF-PA 217.

Remarks and comparisons: Ghoshispora sp. was only recorded in one sample taken at approximately 1 km from the CBN section of the Plesiosaurio locality. Although only a few specimens were recovered, they have all the diagnostic features of the genus. Similar size and sculpture were found in *Ghoshispora bella* (Kondinskaya, 1966) Srivastava, 1978 subsp. *deltoidea* Kutluk et al., 2011 and *Ghoshispora major* (Norton, in Norton and Hall, 1967) Srivastava, 1978, which are characterized for the ribs interconnecting the processes and forming a triangular pattern with distinct lumina. However, in *G. bella* subs. *deltoidea* the processes have a blunt, slightly bent tip whereas in *G. major*, that also has a secondary reticulation within the triangular lumina, the processes are more robust. Both species (*G. bella* subsp. *deltoidea* and *G. major*) have been recorded at the Late Cretaceous of North America (Kutluk et al., 2011).

This constitutes the first record of the genus for Argentina.

Previous record: Ghoshispora has been recorded from Albian to Danian deposits worldwide, although most of the records are from the Northern Hemisphere (Srivastava, 1967; Brenner, 1968; De Lima, 1979; Dettmann, 1995; Kutluk et al., 2011; Batten et al., 2016; among others).

Genus: **Grapnelispora** Stover and Partridge, 1984.

Type species: *Grapnelispora evansii* Stover and Partridge, 1984.

Grapnelispora loncochensis Papú, 1997.

Plate III, 20, 21

Description: Massula with a star-shape, enclosing a trilete microspore. Laesurae extended almost to the equator. Exine psilate, 2–3 μm thick. Perine composed of two layers. Inner layer 10–20 μm thick, with a spongy appearance; outer layer 2 μm thick, psilate. Eight to 12 appendages with hook or anchor-shaped tips extend from the central body. In most cases the appendages have additional hooks along the upper third.

Dimensions: Total length 166 (187) 220 μm (8 specimens measured); microspore diameter 65–77 μm (2 specimens measured); length of appendages 44–82 μm; width of appendages at base 14–32 μm; width of hook or anchor-shaped tips 12–30 μm.

Studied material: MPEF-PA 206 and 654.

Previous record: G. loncochensis is restricted to the Campanian-Maastrichtian of Argentina (Palamarczuk and Gamerro, 1988; Sepúlveda et al., 1989; Papú, 1990, 1993, 1997, 2002; Papú and Sepúlveda, 1995; Marenssi et al., 2004; Vallati, 2010; Puebla et al., 2014).

Genus: **Paleoazolla** Archangelsky, Phipps, Taylor et Taylor 1999 emend. De Benedetti et Zamaloa 2020

Type species: *Paleoazolla patagonica* Archangelsky, Phipps, Taylor et Taylor 1999 emend. De Benedetti et Zamaloa 2020

Paleoazolla patagonica Archangelsky, Phipps, Taylor et Taylor 1999 emend. De Benedetti et Zamaloa 2020

Description: see De Benedetti et al. (2020) for a detailed description.

Studied material: MPEF-PA 86, 100–106, 201–205, 207, 301–319, 580, 586, 587, and 609.

Previous record: Paleoazolla is a monotypic genus known only from the La Colonia Fm., Chubut Province, Argentina. Isolated microspore massulae of *P. patagonica* were reported from the Campanian–Maastrichtian Loncoche Formation, Mendoza Province, Argentina (Puebla et al., 2014). Other possible records of this species based only on microspore massulae were described as *Azollopsis polyancyra* (Stough, 1968) Hall, 1969 from the Late Cretaceous of southern Argentina (see discussion in De Benedetti et al., 2020).

4. Discussion

The macro- and microfossil record of Salviniales in the five studied localities of the La Colonia Fm. is summarized in Table 2 and includes data derived from this study and previous reports. Salvinialean megaspores were recovered only in a few levels of the five studied localities

Plate III. 1–12. *Azollopsis intermedia.* 1. Detail of circular floats enmeshed in perinal hairs and strongly adpressed to the surface of the megaspore apparatus. 2. Cross section of a megaspore apparatus showing exine (*e*) and perine (*p*). 3,4. Cluster of microsporangia. 5. Detail of a microspore massula in a microsporangium. Note the high concentration of circinate glochidia in the contact surfaces of the massulae, while the outer surface is psilate to locally granular and mostly devoid of glochidia. 6. Detail of the non-septate circinate glochidia at LM. 7. Detail of circinate glochidia at SEM. 8. Trilete microspore (detail of 11). 9. Broken massula showing the vacuolated tissue and one microspore with microgranular exine. 10. Microspore massula with about 12 microspores. 11,12. Microspore massula with about eight microspores. 1,2. MPEF-PA 104. 3,4,7,5,9. MPEF-PA 204. 6. MPEF-PA 312. 10. MPEF-PA 306. 8,11. MPEF-PA 311. 12. MPEF-PA 317. 13–17. *Azollopsis tomentosa.* 13. Megaspore apparatus with numerous circular to ovoid floats enmeshed in perinal hairs covering the entire surface. 14. Deteriorate specimen. Note the broken and partially exposed megaspore at bottom and the floats above. 15. Detail of a float (detail of 13). 16. Part of a massula showing one microspore (bottom) and septate multibarbed glochidia (top). 17. Detail of septate multibarbed glochidia. 13,15. MPEF-PA 104. 14. MPEF-PA 201. 16. MPEF-PA 693. 17. MPEF-PA 651. 18,19. *Ghoshispora* sp. Same specimen as LM (18) and SEM (19). MPEF-PA 217. 20,21. *Grapnelispora loncochensis.* Same specimen as LM (20) and SEM (21). MPEF-PA 206. Scale bars: 1,5,10–12 = 20 μm; 2,6-8,15–17 = 10 μm; 3 = 50 μm; 4,13,14 = 100 μm; 9 = 5 μm; 18–21 = 40 μm.

Table 2
Distribution of the Maastrichtian La Colonia Formation Salviniales. Data compiled from this paper and previous records (Archangelsky et al., 1999; Gandolfo et al., 2014; Cúneo et al., 2013, 2014; Hermsen et al., 2013, 2019; De Benedetti et al., 2018, 2020).

Fossil taxa	Cerro Bosta (CBO)			Cañadón del Irupé (CI)			Quebrada del Helecho (QH)			Plesiosaurio (LCP)			Chiva Muerta (CHM)		
	mi	me	M	mi	me	M	mi	me	M	mi	me	M	mi	me	M
Azolla andreisii		+									+				
Azolla coloniensis	+	+		+	+	+	+	+		+	+		+	+	
Azolla sp. 1	+									+			+		
Azollopsis intermedia	+	+								+			+		
Azollopsis tomentosa	+	+													
Crybelosporites pannuceus	+			+						+			+		
Gabonisporis cristata	+									+					
Ghoshispora sp.											+				
Grapnelispora loncochensis													+		
Lugiomarsiglia aquatica						+									
Mirasolita irupensis						+			+						
Molaspora lobata		+			+						+			+	
Molaspora reticulata											+			+	
Paleoazolla patagonica	+	+		+	+		+			+	+		+		
Regnellidium thomas-taylorii			+						+						

mi = microspore/microspore massulae; me = megaspore; M = macrofossil.

while microspores and microspore massulae were consistently recorded in all five sections. The La Colonia Fm. water fern record comprises members of Marsileaceae and Salviniaceae as well as others of uncertain taxonomic placement.

4.1. Family Marsileaceae

Marsileaceae is represented at the La Colonia by two species of microspores, *Crybelosporites pannuceus* and *Gabonisporis cristata* and two species of megaspores, *Molaspora lobata* and *M. reticulata*. These spores were found in the same sediments as leaves of *Regnellidium thomas-taylorii* Cúneo et al., 2013 and *Mirasolita irupensis* Hermsen et al., 2013 and sporocarps of *Lugiomarsiglia aquatica* Gandolfo et al. in Hermsen et al., 2013 but not in organic connection.

M. lobata is practically identical to the megaspores of the extant *Regnellidium diphyllum* Lindman, whereas *C. pannuceus* is morphologically similar to the microspores of modern *Regnellidium* and *Pilularia* (Lupia et al., 2000; Batten et al., 2011a). Interestingly, microspores assignable to *C. pannuceus* have been found attached to *M. lobata* megaspores in Maastrichtian sediments of Spain (Batten et al., 2011a, 2011b), and both spores were also found in-situ in *Regnellidium upatoiensis* Lupia et al., 2000 sporocarps from the Santonian of USA. On the other hand, Aulenback (2009) reported a sporocarp containing megaspores of *Molaspora reticulata* and microspores of *Gabonisporis cristata* (described as *Gabonisporis bacaricumulus* Srivastava) from the Campanian–Maastrichtian of Canada, thus demonstrating the relationship between both micro- and megaspores dispersed taxa. Notably, although not in organic connection, these four species are strongly associated in the sediments of the La Colonia Fm., suggesting that *C. pannuceus* and *M. lobata* were probably produced by the same taxon while *G. cristata* and *M. reticulata* corresponded to another taxon. However, only when found in organic connection this hypothesis can be confirmed.

4.2. Family Salviniaceae

The first *Azolla* species reported from South America corresponds to *A. boliviensis* from the Maastrichtian of Bolivia (Vajda and McLoughlin, 2005). Later, *A. colhuehuapensis* and *A. coloniensis* were described from the Maastrichtian of Patagonia, Argentina (Vallati et al., 2017; De Benedetti et al., 2018; Hermsen et al., 2019). In Argentina, the Late Cretaceous record of *Azolla* is abundant although it is based principally on microspore massulae that, unfortunately, have little or no taxonomic value (Palamarczuk and Gamerro, 1988; Papú, 1988, 1990, 2002; Papú et al., 1988; Quattrocchio et al., 2005; Vallati, 2010; Puebla et al., 2014).

In the La Colonia Fm., Salviniaceae is represented by three *Azolla* species; in addition to *Azolla coloniensis*, *A. andreisii*, a new species based on megaspores and *Azolla* sp. 1, represented by microspore massulae that probably belong to *A. andreisii* are recorded.

4.3. Family incertae sedis

The La Colonia aquatic fern spore assemblage also has representatives of genera that may belong to the *Azolla* and *Salvinia* stem groups or to other lineages in the phylogeny of the Salviniales. Within this group there are: *Azollopsis intermedia, A. tomentosa, Paleoazolla patagonica, Ghoshispora* sp., and *Grapnelispora loncochensis.*

The genus *Azollopsis* is emended here to include megaspore apparatuses containing more than one megaspore, a character observed in numerous specimens of *A. intermedia* derived from samples collected at the Cerro Bosta locality of the La Colonia Formation. As mentioned above, *Azollopsis* was initially reported from the Late Cretaceous and Paleocene of North America, Late Cretaceous of Hungary, Cretaceous and Paleocene sediments of India, and South America. The reports of *Azollopsis intermedia* and *A. tomentosa* megaspores from the La Colonia Fm. represent the first records for both species in the Southern Hemisphere and confirm their wider distribution in the Late Cretaceous. *Paleoazolla* is a monotypic genus known to occur only at the La Colonia Fm., its most remarkable feature is the presence of one to three megaspores per megaspore apparatus (De Benedetti et al., 2020). However, new findings of polymegaspory in *Azollopsis* spores indicate that this feature was not unique to *Paleoazolla*. This is significant as the presence of a single megaspore per megasporangium is considered a characteristic of the order Salviniales, although there are a few cases in which polymegaspory is observed to occur in modern populations of *Azolla* (Strasburger, 1873; Pfeiffer, 1907). Interestingly, *Paleoazolla*, *Azollopsis*, and *Azolla* not only share polymegaspory but also other morphological characters, such as the presence of filosum, a vacuolated perine, and microspores arranged in massulae with anchor-shaped or circinate glochidia, that strongly support their intimate relationships.

The genus *Ghoshispora* is almost worldwide distributed and practically restricted to the Cretaceous of the Northern Hemisphere (Kutluk et al., 2011; Batten et al., 2016). There is only one species from South America, *Ghoshispora minuta* (Brenner, 1968) Kutluk et al., 2011, from the Albian of Perú (Brenner, 1968; Kutluk et al., 2011) and the Aptian-Albian of northeastern Brazil (De Lima, 1979; Batten, 2007). The

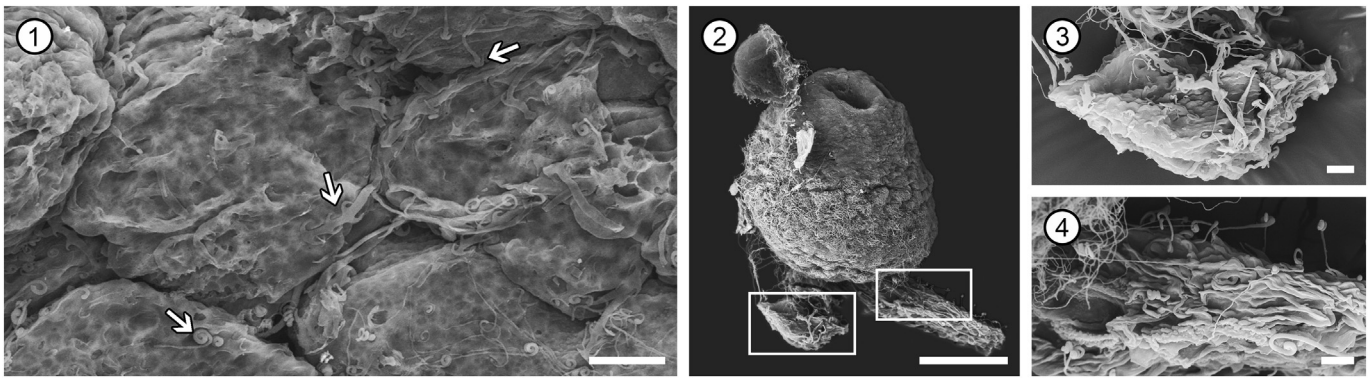


Plate IV. 1. Cluster with different types of massulae, including *Azolla coloniensis*, *Azollopsis intermedia*, and *Paleoazolla patagonica*. Note different types of glochidia (*arrows*). MPEF-PA 207. 2. *Azolla coloniensis* megaspore with attached microspore massulae of *Paleoazolla patagonica* (detail in 3) and *Azollopsis intermedia* (detail in 4). MPEF-PA 204. Scale bars: 1 = 20 μm; 2 = 100 μm; 3,4 = 10 μm.

specimens described here as *Ghoshispora* sp. represent the southernmost record for the genus and the first mention for Argentina. As mentioned before, Aulenback (2009) reported fossil fern sporophytes containing *Ghoshispora* mega- and microspores, and he suggested that this fossil probably corresponds to an extinct lineage related to *Salvinia*.

The genus *Grapnelispora* was originally described as a megaspore by Stover and Partridge (1984). However, due to the presence of appendages with anchor-like tips, it was also interpreted as a salviniaceous massula containing only one microspore (Palamarczuk and Gamerro, 1988; Papú, 1993, 1997). This is the first record of the genus at the La Colonia Fm.

4.4. Comparison of the Salviniales record among the La Colonia Fm. localities

Distinctly, the species of Salviniales studied here have different distributions among the five localities (Table 2). Such differences may be linked to multiple contributing factors such as the relative abundance of each species in the past communities, differences in the environmental preferences and ecological tolerance of the species, preservational biases, etc. Overall, LCO and CBO are the localities with higher species diversity.

Azolla coloniensis and *Paleoazolla patagonica* are the most widely distributed species being present at the five studied localities. The new species *Azolla andreisii* (and their probably associated microspores of *A.* sp. 1) was recorded only in the CBO and LCP localities. Among the *Azollopsis* species, *A. intermedia* was recorded in three (CBO, LCP, and CHM) of the five localities whereas *A. tomentosa* was only recorded at the CBO locality. Spores of *Paleoazolla*, *Azolla*, and *Azollopsis* are extremely abundant in some levels of the La Colonia sediments where clusters made up of different types of microspore massulae are frequent (Plate IV, 1), as well as megaspores with massulae of different species of microspores attached to the same megaspore body (Plate IV, 2–4).

Among the marsileaceous spores, *Molaspora lobata* and the associated microspores *Crybelosporites pannuceus* were recorded in four (CBO, CI, LCP, and CHM) localities, while *Molaspora reticulata* and the associated microspores *Gabonisporis cristata* were recorded only in two (LCP and CHM) localities. *Ghoshispora* sp. and *Grapnelispora loncochensis* are rare species and are scarcely represented in one locality each, LCP and CHM respectively.

During the Late Cretaceous, extensive areas of Southern South America were covered by shallow epicontinental seas giving place to the formation of a series of coastal plain sedimentary deposits representing estuaries, deltas, and lagoon/barrier complexes (Scasso et al., 2012; Gandolfo et al., 2014; Cúneo et al., 2014). It was in this scenario that the La Colonia and other coeval formations were deposited (Spalletti, 1996; Page et al., 1999; Malumián and Náñez, 2011; Scasso et al., 2012; Figari et al., 2015). The high diversity and abundance of Salvinialean spores reported here for several localities of the La Colonia Fm. suggest that this group played an important role in the plant communities that grew at the Late Cretaceous Patagonian wetlands.

5. Conclusions

We present a highly diverse water fern spore assemblage recovered from the Maastrichtian of the La Colonia Formation, Patagonia, Argentina. The assemblage comprises members of both families of the Salviniales and others of uncertain placement within the group. Within Marsileaceae, in addition to the *Molaspora lobata* megaspores and associated microspores of *Crybelosporites pannuceus* previously known to occur at the formation, we recognize *Molaspora reticulata* megaspores and associated microspores of *Gabonisporis cristata*, that constitute the first record for both species in the Southern Hemisphere, extending notably the geographic range of these species and increasing the diversity of both genera in Patagonia. For Salviniaceae, besides *Azolla coloniensis*, we document the new species *Azolla andreisii*, that constitutes the fourth species identified for the genus from the Late Cretaceous of South America and expanding its diversity for the Maastrichtian of Patagonia. Salvinialean spores of uncertain family placement include *Azollopsis intermedia*, *A. tomentosa*, *Ghoshispora* sp., *Grapnelispora loncochensis*, and *Paleoazolla patagonica*. We introduce the southernmost record of genus *Ghoshispora*, which constitutes the first mention for Argentina. We register megaspores of *Azollopsis intermedia* and *A. tomentosa* for first time in Late Cretaceous of the Southern Hemisphere. Furthermore, we emended *Azollopsis* to include megaspore apparatuses with more than one megaspore. This remarkable feature, polymegaspory, was originally recognized in *Paleoazolla*. Surprisingly, except for a few mentions in modern *Azolla*, polymegaspory has only been registered in the Southern Hemisphere fossil record, which leaves us with more questions than answers, among them: Is polymegaspory a character unique to Southern Hemisphere taxa?, is it a rare phenomenon that simply occurs(ed) in a reduced number of individuals in a population as in modern *Azolla*?, is it related to particular environmental conditions?, and is it due to misinterpretation of the complete megasporangium content?, is it only detected by different techniques (clearing of the whole megaspore complex, longitudinal sections, etc.)?

Clearly, the La Colonia deposits have extraordinary potential to preserve both macro- and microfossils denoting the necessity of expanding fieldwork that will definitely contribute to better assessment of evolutionary aspects of the water ferns (e.g., polymegaspory), but also biogeography, diversification, distribution patterns, etc. In summary, the emergent Southern Hemisphere record of the water ferns provides significant contributions to the high diversity of the group and on crucial

morphological data to be considered in phylogenetic studies, not only of heterosporous ferns but of all vascular plants as well.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors thank M. Caffa, L. Canessa, C. Gonzalez, E.J. Hermsen, P. Puerta, L. Reiner, E. Ruigomez, P. Wilf and many others for assistance during field and laboratory work. Richard Lupia, an anonymous reviewer, and the editor are specially thanked for their helpful comments and suggestions. This research was supported in part by NSF grants DEB-1556666, DEB-1556136, DEB-0919071, DEB-0918932, and EAR-1925552.

Appendix. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.revpalbo.2021.104428.

References

Anselmi, G., Gamba, M.T., Panza, J.L.A., 2004. Hoja Geológica 4369-IV. Los Altares. Provincia de Chubut. Servicio Geológico Minero Argentino. Instituto de Geología y Recursos Minerales, Buenos Aires, Boletín 313, 1–98.
Archangelsky, A., Phipps, C.J., Taylor, T.N., Taylor, E.L., 1999. *Paleoazolla*, a new heterosporous fern from the Upper Cretaceous of Argentina. Am. J. Bot. 86, 1200–1206.
Ardolino, A.A., Franchi, M., 1996. Hoja Geológica 4366-I. Telsen. Provincia de Chubut. Subsecretaría de Minería de la Nación. Dirección Nacional del Servicio Geológico, Buenos Aires, Boletín 215, 1–110.
Arnold, C.A., 1955. A Tertiary *Azolla* from British Columbia. Contributions from the Museum of Paleontology, University of Michigan, XII 4, 37–45.
Aulenback, K.R., 2009. Identification Guide to the Fossil Plants of the Horseshoe Canyon Formation of Drumheller, Alberta. University of Calgary Press, Alberta.
Baldoni, A.M., Batten, D.J., 1997. Cretaceous megaspores from two boreholes in the Austral Basin, Santa Cruz Province, Argentina, and their stratigraphic and palaeoenvironmental significance. Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen 205, 97–110.
Barreda, V.D., Cúneo, N.R., Wilf, P., Currano, E.D., Scasso, R.A., Brinkhuis, H., 2012. Cretaceous/Paleogene floral turnover in Patagonia: drop in diversity, low extinction, and a *Classopollis* spike. PLoS One 7 (12), e52455.
Batten, D.J., 1987. Revision of S.J. Dijkstra's late Cretaceous megaspores and other plant microfossils from Limbourg, The Netherlands. Med. Rijks Geol. Dienst. 41, 1–55.
Batten, D.J., 2007. Spores and pollen from the Crato Formation: biostratigraphic and palaeoenvironmental implications. The Crato fossil beds of Brazil: window into an ancient world. Cambridge University Press, Cambridge, pp. 566–573.
Batten, D.J., Collinson, M.E., 2001. Revision of species of *Minerisporites*, *Azolla* and associated plant microfossils from deposits of the Upper Palaeocene and Palaeocene/Eocene transition in the Netherlands, Belgium and the USA. Rev. Palaeobot. Palynol. 115, 1–32.
Batten, D.J., Kovach, W.L., 1990. Catalog of Mesozoic and Tertiary megaspores. American Association of Stratigraphic Palynologists Foundation; Contribution Series 24, 1–227.
Batten, D.J., Collinson, M.E., Brain, A.P.R., 2011a. Megaspores and microspores of the extant and Paleogene marsileaceous fern *Regnellidium* and Cretaceous *Molaspora*: evolutionary and phytogeographic implications. Int. J. Plant Sci. 172, 1087–1100.
Batten, D.J., Zavattieri, A.M., Collinson, M.E., 2011b. Megaspores from the upper Maastrichtian of the eastern Spanish Pyrenees and their biostratigraphic, palaeogeographic and palaeoenvironmental significance. Rev. Palaeobot. Palynol. 167, 156–172.
Batten, D.J., Li, J., Peng, J., 2016. Megaspores attributable to *Ghoshispora* in Late Cretaceous deposits of the Songliao Basin, north-east China: taxonomic clarification and distribution. Rev. Palaeobot. Palynol. 232, 40–60.
Boltenhagen, E., 1967. Pollen et spores du Crétacé Supérieur du Gabon. Pollen Spores 9, 335–355.
Braman, D.R., 2018. Terrestrial palynostratigraphy of the Upper Cretaceous (Santonian) to lowermost Paleocene of southern Alberta, Canada. Palynology 42, 102–147.
Brenner, G.J., 1963. The spores and pollen of the Potomac Group of Maryland. Department of Geology, Mines and Water Resources. Maryland. Bulletin 27, 1–215.
Brenner, G.J., 1968. Middle Cretaceous spores and pollen from northeastern Peru. Pollen Spores 10, 341–383.
Campbell, J.D., Untergasser, B., 1972. Two new megaspore species from the continental Upper Cretaceous (Campanian–Maestrichtian) of the Alberta Plains. Can. J. Bot. 50, 2553–2557.
Collinson, M.E., 1980. A new multiple-floated *Azolla* from the Eocene of Britain with a brief review of the genus. Palaeontology 23, 213–229.
Collinson, M.E., 1991. Diversification of modern heterosporous pteridophytes. In: Blackmore, S., Barnes, S.H. (Eds.), Pollen and spores: patterns of diversification. 44. Systematics Association. Clarendon Press, Oxford, pp. 119–150 Special Vol.
Collinson, M.E., 2001. Cainozoic ferns and their distribution. Brittonia 53, 173–235.
Collinson, M.E., Barke, J., van der Burgh, J., van Konijnenburg-van Cittert, J.H., 2009. A new species of the freshwater fern Azolla (Azollaceae) from the Eocene Arctic Ocean. Rev. Palaeobot. Palynol. 155, 1–14.
Collinson, M.E., Smith, S.Y., van Konijnenburg-van Cittert, J.H., Batten, D.J., van der Burgh, J., Barke, J., Marone, F., 2013. New observations and synthesis of Paleogene heterosporous water ferns. Int. J. Plant Sci. 174, 350–363.
Collinson, M.E., Van Konijnenburg-Van Cittert, J.H., Marone, F., Brain, A.P., 2017. Reinterpretation of *Azolla primaeva* (Azollaceae, Eocene, Canada) using electron microscopy and X-ray tomographic microscopy. Rev. Palaeobot. Palynol. 240, 33–48.
Cookson, I.C., Dettmann, M.E., 1958. Cretaceous "megaspores" and a closely associated microspores from the Australian region. Micropaleontology 4, 39–49.
Cúneo, N.R., Hermsen, E.J., Gandolfo, M.A., 2013. *Regnellidium* (Salviniales, Marsileaceae) macrofossils and associated spores from the Late Cretaceous of South America. Int. J. Plant Sci. 174, 340–349.
Cúneo, N.R., Gandolfo, M.A., Zamaloa, M.C., Hermsen, E.J., 2014. Late Cretaceous Aquatic Plant World in Patagonia, Argentina. PLoS One 9 (8), e104749.
De Benedetti, F., Zamaloa, M.C., Gandolfo, M.A., Cúneo, N.R., 2018. Heterosporous ferns from Patagonia: the case of *Azolla*. In: Krings, M., Harper, C.J., Cúneo, N.R., Rothwell, G.W. (Eds.), Transformative Paleobotany. Academic Press, London, pp. 361–373.
De Benedetti, F., Zamaloa, M.C., Gandolfo, M.A., Cúneo, N.R., 2020. Reinterpretation of *Paleoazolla*: a heterosporous water fern from the Late Cretaceous of Patagonia, Argentina. Am. J. Bot. 107, 1–18.
De Lima, M.R., 1979. Palinologia da Formacão Santana (Cretáceo do nordeste do Brasil). II. Descricão sistemática dos esporos da subturma zonotriletes e turma monolotes, e dos polens das turmas saccites e aletes. Ameghiniana 16, 27–63.
Dettmann, M.E., 1963. Upper Mesozoic microfloras from south-eastern Australia. Proc. R. Soc. Victoria 77, 1–148.
Dettmann, M.E., 1995. Ultrastructure and biogeography of *Balmeisporites* Cookson and Dettmann, 1958. Rev. Palaeobot. Palynol. 89, 287–296.
Dijkstra, S.J., 1949. Megaspores and some other fossils from the Aachenian (Senonian) of South Limburg, Netherlands. Mededeelingen van de Geologische Stichting, Nieuwe Serie 3, 19–32.
Dijkstra, S.J., 1961. Some Paleocene megaspores and other small fossils. Mededeelingen van de Geologische Stichting, Nieuwe Serie 13, 5–12.
Estrada-Ruiz, E., Centeno-Gonzalez, N.K., Aguilar-Arellano, F., Martinez-Cabrera, H.I., 2018. New record of the aquatic fern *Marsilea*, from the Olmos Formation (Upper Campanian), Coahuila, Mexico. Int. J. Plant Sci. 179, 487–496.
Figari, C.E., Scasso, R.A., Cúneo, N.R., Escapa, I.H., 2015. Estratigrafía y evolución geológica de la Cuenca de Cañadón Asfalto, Provincia del Chubut, Argentina. Latin Am. J. Sedimentol. Basin Anal. 22, 135–169.
Florschütz, F., 1945. *Azolla* uit het Nederlandsche Palaeoceen en Pleistoceen. Verhandelingen van het Geologisch Mijnbouwkundig Genootschap voor Nederland en Koloniën, Geologisch Serie 14, 191–198.
Fowler, K., Stennett-Willson, J., 1978. Sporoderm architecture in modern *Azolla*. Fern Gazette 11, 405–412.
Gandolfo, M.A., Cúneo, N.R., Hermsen, E.J., 2014. Reporte preliminar sobre la paleoflora de la Formación La Colonia (Campaniano-Maastrichtiano, Cretácico tardío), Chubut, Patagonia, Argentina. Bol. Soc. Geol. Mex. 66, 11–23.
Guler, M.V., Borel, C.M., Brinkhuis, H., Navarro, E., Astini, R., 2014. Brackish to freshwater dinoflagellate cyst assemblages from the La Colonia Formation (Paleocene), Northeastern Patagonia, Argentina. Ameghiniana 51, 141–153.
Gunther, P.R., Hills, L.V., 1972. Megaspores and other palynomorphs of the Brazeau formation (Upper Cretaceous), Nordegg area, Alberta. Geoscience and Man 4, 29–48.
Hall, J.W., 1963. Megaspores and other fossils in the Dakota Formation (Cenomanian) of Iowa, (USA). Pollen Spores 5, 425–443.
Hall, J.W., 1968. A new genus of Salviniaceae and a new species of *Azolla* from the Late Cretaceous. Am. Fern J. 58, 77–88.
Hall, J.W., 1969. Notes on fossil Salviniaceae. Taxon 18, 735.
Hall, J.W., 1974. Cretaceous Salviniaceae. Ann. Mo. Bot. Gard. 61, 354–367.
Hall, J.W., Bergad, R.D., 1971. A critical study of three Cretaceous salviniaceous megaspores. Micropaleontology 17, 345–356.
Hall, J.W., Peake, N.M., 1968. Megaspore assemblages in the Cretaceous of Minnesota. Micropaleontology 14, 456–464.
Hall, J.W., Swanson, N.P., 1968. Studies on fossil *Azolla*: *Azolla montana*, a Cretaceous megaspore with many small floats. Am. J. Bot. 55, 1055–1061.
Hermsen, E.J., 2019. Revisions to the fossil sporophyte record of *Marsilea*. Acta Palaeobot. 59, 27–50.
Hermsen, E.J., Gandolfo, M.A., Cúneo, N.R., 2013. New marsileaceous fossils from the Late Cretaceous of South America and a reevaluation of *Marsileaceaephyllum*. Plant Syst. Evol. 300, 369–386.
Hermsen, E.J., Jud, N.A., De Benedetti, F., Gandolfo, M.A., 2019. *Azolla* Sporophytes and Spores from the Late Cretaceous and Paleocene of Patagonia, Argentina. Int. J. Plant Sci. 180, 737–754.
Herngreen, G.F.W., 1973. Palynology of Albian-Cenomanian strata of Borehole 1-QS-1-MA, state of Maranhao, Brazil. Pollen Spores 15, 515–555.
Hills, L.V., Gopal, B., 1967. *Azolla primaeva* and its phylogenetic significance. Can. J. Bot. 45, 1179–1191.
Hills, L., Weiner, N., 1965. *Azolla geneseana*, n. sp., and revision of *Azolla primaeva*. Micropaleontology 11, 255–261.

Hoffman, G.L., Stockey, R.A., 1994. Sporophytes, megaspores, and massulae of *Azolla stanleyi* from the Paleocene Joffre Bridge locality, Alberta. Can. J. Bot. 72, 301–308.
Ibrahim, M.I.A., Ela, N.A., Kholeif, S.E., 2001. Palynostratigraphy of Jurassic to Lower Cretaceous sequences from the Eastern Desert of Egypt. J. Afr. Earth Sci. 32, 269–297.
Jain, R.K., 1971. Pre-Tertiary records of Salviniaceae. Am. J. Bot. 58, 487–496.
Jain, R.K., Hall, J.W., 1969. A contribution to the early Tertiary fossil record of the Salviniaceae. Am. J. Bot. 56, 527–539.
Kempf, E.K., 1969. Elektronen mikroskopie der megasporen von *Azolla tegeliensis* aus dem Altpleistozän der Niederlande. Palaeontographica 128B, 167–179.
Kondinskaya, L.I., 1966. Fossil spores of water ferns in Upper Cretaceous and Paleogene deposits of the West Siberian Lowland. In: Chlonova, A.F. (Ed.), Palynology of Siberia. Izdatel'stvo "Nauka" Moskva, Akademiya Nauk SSSR, Sibirskoye Otdeleniye. Institut Geologii i Geofiziki, pp. 116–122 3 pls. (in Russian).
Kotova, I.Z., 1978. Spores and pollen from cretaceous deposits of the eastern North Atlantic Ocean, Deep Sea Drilling Project, leg 41, sites 367 and 370. Initial Rep. Deep Sea Drill. Proj. 41, 841–881.
Kovach, W.L., Batten, D.J., 1989. Worldwide stratigraphic occurrences of Mesozoic and Tertiary megaspores. Palynology 13, 247–277.
Kutluk, H., Hills, L.V., 2015. Megaspores from the Upper Cretaceous (Campanian) Horseshoe Canyon Formation of south-central Alberta, Canada, with a review of the genera *Costatheca* and *Spermatites*. Palynology 41, 31–71.
Kutluk, H., Speelman, J.D., Hills, L.V., 2011. The fossil spore genus *Ghoshispora*. Palaeontogr. B 284, 81–123.
Lamarck, J.B., 1783. Encyclopédie Méthodique. Botanique, p. 343.
Li, J., Wu, Y., Peng, J., Batten, D.J., 2019. Palynofloral evolution on the northern margin of the Indian Plate, southern Xizang, China during the Cretaceous period and its phytogeographic significance. Palaeogeogr. Palaeoclimatol. Palaeoecol. 515, 107–122.
Link, H.F., 1833. Hortus Regius Botanicus Berolinensis. Tomus 2, G. Reimer, Berlin, p. 390.
Lupia, R., 2011. Late Santonian megaspore floras from the Gulf Coastal Plain (Georgia, USA). J. Paleontol. 85, 1–21.
Lupia, R., Schneider, H., Moeser, G.M., Pryer, K.M., Crane, P.R., 2000. Marsileaceae sporocarps and spores from the Late Cretaceous of Georgia, U.S.a. Int. J. Plant Sci. 161, 975–988.
Mahmoud, M.S., Schrank, E., 2007. Late Cretaceous spores, pollen and dinoflagellates from two boreholes (Nuqra-1 and 3) in the Aswan area, southeast Egypt. Rev. Paléobiol. 26, 593–613.
Malumián, N., Náñez, C., 2011. The Late Cretaceous-Cenozoic transgressions in Patagonia and the Fuegian Andes: foraminifera, palaeoecology, and palaeogeography. Biol. J. Linn. Soc. 103, 269–288.
Malumián, N., Náñez, C., Caramés, A., 1991. Unilocular foraminifera of reticular surface from Argentina. Micropaleontology 37, 393–406.
Marenssi, S., Guler, V., Casadío, S., Guerstein, R., Papú, O., 2004. Sedimentology and palynology of the Calafate Formation (Maastrichtian), Austral Basin, Southern Patagonia, Argentina. Cretaceous Res. 25, 907–918.
Martin, A.R.H., 1976a. Upper Paleocene Salviniaceae from the Woolwich/Reading Beds near Cobham, Kent. Paleontology 19, 173–184.
Martin, A.R.H., 1976b. Some structures in *Azolla* megaspores, and an anomalous form. Review of Palaeobotany and Palynology 21, 141–169.
Martinov, I.I., 1820. Tekhno-botanicheskii slovar. p. 559.
McIver, E.E., Basinger, J.F., 1993. Flora of the Ravenscrag formation (Paleocene), Southwestern Saskatchewan, Canada. Palaeontogr. Can. 10, 1–167.
Melchior, R.C., Hall, J.W., 1983. Some megaspores and other small fossils from the Wannagan Creek site (Paleocene), North Dakota. Palynology 7, 133–145.
Mirbel, C.F.B., 1802. Marsileaceae. Histoire naturelle des végétaux classés par familles avec la citation de la classe et de l'ordre de Linné, et l'indication de l'usage que l'on peut faire des plantes dans les arts, le commerce, l'agriculture, le jardinage, la médecine, etc. des figures dessinées d'aprè s nature, et un genera complet, selon le systè me de Linné, avec des renvois aux familles naturelles de A.L. de Jussieu 5. De l'imprimerie de Crapelet; chez Deterville, Paris, p. 126.
Nagalingum, N.S., Schneider, H., Pryer, K.M., 2006. Comparative morphology of reproductive structures in heterosporous water ferns and a reevaluation of the sporocarp. Int. J. Plant Sci. 167, 805–815.
Nandi, B., Chattopadhyay, S., 2003. Heterosporous water ferns from the Late Cretaceous to Neogene periods of India. Pteridology in the New Millennium. Springer, Dordrecht, pp. 505–520.
Náñez, C., Malumián, N., 2008. Paleobiogeografía y paleogeografía del Maastrichtiense marino de la Patagonia, Tierra del Fuego y la Plataforma Continental Argentina, según sus foraminíferos bentónicos. Rev. Esp. Paleontol. 23, 273–300.
Norton, N.J., Hall, J.W., 1967. Guide sporomorphae in the Upper Cretaceous-lower Tertiary of eastern Montana (USA). Rev. Palaeobot. Palynol. 2, 99–110.
Page, R., Ardolino, A., de Barrio, R.E., Franchi, M., Lizuain, A., Page, S., Silva Nieto, D., 1999. Estratigrafía del Jurásico y Cretácico del Macizo de Somún Curá, provincias de Río Negro y Chubut. In: Caminos R. (Ed.), Geología Regional Argentina, Servicio Geológico Minero Argentino. Instituto de Geología y Recursos Minerales, Buenos Aires. Anales 29, 460–488.
Palamarczuk, S., Gamerro, J.C., 1988. Grapnelispora evansii megaspora del Cretácico Superior (?Campaniano Superior-Maastrichtiano) de la Argentina y Antártida. IV Congreso Argentino de Paleontología y Bioestratigrafía, Mendoza, Argentina. Actas. 3, pp. 87–93.
Papú, O.H., 1988. Estudio palinológico de la Formación Paso del Sapo (Cretácico Superior) en la localidad "Los Fortines", valle medio del río Chubut. Parte II. Esporas triletes Muronati, Tricrassati y esporas monoletes. IV Congreso Argentino de Paleontología y Bioestratigrafía, Mendoza, Argentina. Actas. 3, pp. 75–85.
Papú, O.H., 1990. Contribución a la palinología estratigráfica de la Formación Malargüe, Cretácico Superior, sur de la provincia de Mendoza, Argentina. Parte I: Especies terrestres y de aguas continentales. Ameghiniana 27, 289–303.
Papú, O.H., 1993. Nuevos hallazgos del género *Grapnelispora* (Stover & Partridge) en la Formación Loncoche de Ranquil-Co, Cretácico Superior en la provincia de Mendoza, Argentina. Ameghiniana 30, 143–147.
Papú, O.H., 1997. Nueva especie de *Grapnelispora* del Campaniense-Maastrichtiense, provincia de Mendoza, Argentina. Inferencias filogenéticas, paleobiogeográficas y paleoambientales. Rev. Esp. Paleontol. 12, 197–205.
Papú, O.H., 2002. Nueva microflora de edadmaastrichtiana en la localidad de Calmu-Co, sur de Mendoza, Argentina. Ameghiniana 39, 415–426.
Papú, O.H., Sepúlveda, E., 1995. Datos palinológicos de la Formación Los Alamitos en la localidad de Montoniló, Departamento de 25 de Mayo, Río Negro, Argentina. Sus relaciones con unidades colindantes coetáneas. VI Congreso Argentino de Paleontología y Bioestratigrafía, Actas, pp. 195–200.
Papú, O.H., Volkheimer, W., Sepúlveda, E.G., 1988. Másulas de Salviniaceae del Cretácico Tardío de Nordpatagonia y sur de Mendoza, Argentina. Su importancia bioestratigráfica y paleoambiental. V Congreso Geológico Chileno, III, pp. H67–H81.
Penhallow, D.P., 1908. Report on Tertiary Plants of British Columbia collected by Lawrence M. Lambe in 1906: together with a Discussion of Previously Recorded Tertiary Floras. Canada Department of Mines and Resources, Geological Survey British Columbia, No. 1013, Ottawa.
Peyrot, D., Playford, G., Mantle, D.J., Backhouse, J., Milne, L.A., Carpenter, R.J., Foster, C., Mory, A.j., McLoughlin, S., Vitacca, J., Scibiorski, J., Mack, C.L., Bevan, J., 2019. The greening of Western Australian landscapes: the Phanerozoic plant record. J. R. Soc. West. Aust. 102, 52–82.
Pfeiffer, W.M., 1907. Differentiation of sporocarps in Azolla. Bot. Gaz. 44, 445–454.
PPG I [The Pteridophyte Phylogeny Group], 2016. A community-derived classification for extant lycophytes and ferns. J. Syst. Evol. 54, 563–603.
Puebla, G.G., Prámparo, M.B., Gandolfo, M.A., 2014. Aquatic ferns from the Upper Cretaceous Loncoche Formation, Mendoza, central-western, Argentina. Plant Syst. Evol. 301, 577–588.
Quattrocchio, M.E., Volkheimer, W., Marquillas, R.A., Salfity, J.A., 2005. Palynostratigraphy, palaeobiogeography and evolutionary significance of the Late Senonian and Early Palaeogene palynofloras of the Salta Group, northern Argentina. Rev. Esp. Micropaleontol. 37, 259–272.
Rai, S., Sharma, P., 2004. Palynological assemblage from the Anjar intertrappeans, Kutch district, Gujarat: age implications. Curr. Sci. 86, 1596–1597.
Rákosi, L., Barbacka, M., 2000. Upper Cretaceous flora from Ajka (W Hungary). I. Thallophyta. Studia Bot. Hung. 30, 27–55.
Rouse, G.E., 1962. Plant microfossils from the Burrard Formation of western British Columbia. Micropaleontology 8, 187–218.
Sacomani, L.E., Panza, J.L.A., Parisi, C., Pezzuchi, H.D., Ardolino, A.A., 2007. Hoja Geológica 4366-III. Las Plumas. Servicio Geológico Minero Argentino. Instituto de Geología y Recursos Minerales. Buenos Aires. Boletín 291, 1–74.
Salard-Cheboldaeff, M., 1990. Intertropical African palynostratigraphy from Cretaceous to late Quaternary times. J. Afr. Earth Sci. (Middle East) 11, 1–24.
Samant, B., Mohabey, D.M., Kapgate, D.K., 2008. Palynofloral record from Singpur intertrappean, Chhindwara district, Madhya Pradesh: implication for late cretaceous stratigraphic correlation and resolution. J. Geol. Soc. India 71, 851–858.
Santamarina, P.E., Barreda, V.D., Iglesias, A., Varela, A.N., 2018. Salvinialean megaspores in the Late Cretaceous of southern Patagonia, Argentina. Acta Palaeontologica Polonica 63, 607–616.
Scafati, L., Melendi, D.L., Volkheimer, W., 2009. A Danian subtropical lacustrine palynobiota from South America (Bororo Formation, San Jorge Basin, Patagonia-Argentina). Geol. Acta Int. Earth Sci. J. 7, 35–61.
Scasso, R.A., Aberhan, M., Ruiz, L., Weidemeyer, S., Medina, F.A., Kiessling, W., 2012. Integrated bio-and lithofacies analysis of coarse-grained, tide-dominated deltaic environments across the Cretaceous/Paleogene boundary in Patagonia, Argentina. Cretac. Res. 36, 37–57.
Schemel, M.P., 1950. Cretaceous plant microfossils from Iowa. Am. J. Bot. 37, 750–754.
Schneider, H., Pryer, K.M., 2002. Structure and function of spores in the aquatic heterosporous fern family Marsileaceae. Int. J. Plant Sci. 163, 485–505.
Sepúlveda, E.G., Papú, O.H., Volkheimer, W., 1989. Importancia estratigráfica y paleobiogeografica del género *Grapnelispora* Stover & Partridge en el Cretácico Tardío del hemisferio austral. Boletim Instituto de Geociências Universidade de São Paulo, Publicação Especial 7, 163–171.
Smith, A.R., Pryer, K.M., Schuettpelz, E., Korall, P., Schneider, H., Wolf, P.G., 2006. A classification for extant ferns. Taxon 55, 705–731.
Snead, R.G., 1969. Microfloral diagnosis of the Cretaceous-Tertiary boundary, Central Alberta. Res. Coun. Alberta Bull. 25, 1–148.
Spalletti, L.A., 1996. Estuarine and shallow-marine sedimentation in the Upper Cretaceous-lower Tertiary west-central Patagonian Basin (Argentina). In: de Batist, M., Jacobs, P. (Eds.), Geology of Siliciclastic Shelf Seas. Geological Society of London, Special Publication vol. 117, pp. 81–93.
Speelman, J.D., Hills, L.V., 1980. Megaspore paleoecology: Pakowki, Foremost and Oldman formations (Upper Cretaceous), southeastern Alberta. Bull. Can. Petrol. Geol. 28, 522–541.
Srivastava, S.K., 1967. Upper Cretaceous microflora (Maestrichtian) from Scollard, Alberta, Canada. Pollen Spores 8, 497–552.
Srivastava, S.K., 1968. *Azolla* from the Upper Cretaceous Edmonton Formation, Alberta, Canada. Can. J. Earth Sci. 5, 915–919.
Srivastava, S.K., 1972. Systematic description of some spores from the Edmonton Formation (Maestrichtian), Alberta, Canada. Palaeontogr. B 139, 1–46.
Srivastava, S.K., 1977. Microspores from the Fredericksburg Group (Albian) of the southern United States. Paléobiologie Continentale 6, 1–119.
Srivastava, S.K., 1978. The Cretaceous megaspore genus *Ghoshispora*. Palaeontogr. B 167, 175–184.

Srivastava, S.K., Braman, D.R., 2013. The palynostratigraphy of the Edmonton Group (Upper Cretaceous) of Alberta, Canada. Palynology 37, 1–27.
Stanley, E.A., 1965. Upper cretaceous and Paleocene plant microfossils and Paleocene dinoflagellates and hystrichosphaerids from northwestern South Dakota. Bull. Am. Paleontol. 49, 1–384.
Stough, J.B., 1968. Palynomorphs from South America. Univ. Kansas Publ. 32, 1–12.
Stover, L.E., Partridge, A.D., 1984. A new late cretaceous megaspore with grapnel-like appendage tips from Australia and New Zealand. Palynology 8, 139–144.
Strasburger, E., 1873. Ueber *Azolla*. Jena, Hermann Dabis.
Sweet, A.R., 1986. The Cretaceous-Tertiary boundary in the central Alberta FoothillsII: Miospore and pollen taxonomy. Can. J. Earth Sci. 23, 1375–1388.
Sweet, A.R., Chandrasekharam, A., 1973. Vegetative remains of *Azolla schopfii* Dijkstra from Genesee, Alberta. Can. J. Bot. 51, 1491–1496.
Sweet, A.R., Hills, L.V., 1974. A detailed study of the genus *Azollopsis*. Can. J. Bot. 52, 1625–1642.
Sweet, A.R., Hills, L.V., 1976. Early Tertiary species of *Azolla* subg. *Azolla* sect. *Kremastospora* from western and arctic Canada. Can. J. Bot. 54, 334–351.
Takahashi, M., Crane, P.R., Ando, H., 2001. Fossil megaspores of Marsileales and Selaginellales from the upper Coniacian to lower Santonian (Upper Cretaceous) of the Tamagawa Formation (Kuji Group) in northeastern Japan. Int. J. Plant Sci. 162, 431–439.
Tryon, A.F., Lugardon, B., 1991. Spores of the Pteridophyta. Surface, Wall Structure, and Diversity Based on Electron Microscope Studies. Springer-Verlag, New York, NY, USA.
Vajda, V., McLoughlin, S., 2005. A new Maastrichtian-Paleocene *Azolla* species from Bolivia, with a comparison of the global record of coeval *Azolla* microfossils. Alcheringa 29, 305–329.
Vallati, P., 2010. Asociaciones palinológicas con angiospermas en el Cretácico Superior de la Cuenca Neuquina, Argentina. Rev. Brasil. Paleontol. 13, 143–158.
Vallati, P., Casal, G., Foix, N., Allard, J., Tomas, A.D.S., Calo, M., 2016. First report of a Maastrichtian palynoflora from the Golfo San Jorge Basin, central Patagonia, Argentina. Ameghiniana 53, 495–505.
Vallati, P., De Sosa Tomas, A., Casal, G., Calo, M., 2017. Salviniales from the Late Cretaceous of the Golfo San Jorge Basin. Cretac. Res. 74, 45–55.
Van der Burgh, J., Collinson, M.E., van Konijnenburg-van Cittert, J.H., Barke, J., Brinkhuis, H., 2013. The freshwater fern *Azolla* (Azollaceae) from Eocene Arctic and Nordic Sea sediments: new species and their stratigraphic distribution. Rev. Palaeobot. Palynol. 194, 50–68.
Venkatachala, B.S., Sharma, K.D., 1974. Palynology of the Cretaceous sediments from the subsurface of Pondicherry area, Cauvery Basin. New Bot. 1, 170–200.
Villanueva-Amadoz, U., Sender, L.M., Diez, J.B., Ferrer, J., Pons, D., 2011. Palynological studies of the boundary marls unit (Albian-Cenomanian) from northeastern Spain. Paleophytogeographical implications. Geodiversitas 33, 137–176.
Villar de Seoane, L., Archangelsky, S., 2008. Taxonomy and biostratigraphy of Cretaceous megaspores from Patagonia, Argentina. Cretac. Res. 29, 354–372.
Villar de Seoane, L., Archangelsky, S., 2013. Ultrastructural study of *Arcellites humilis* Villar de Seoane and Archangelsky, 2008, from the Cretaceous of Patagonia, Argentina. Geobios 46, 243–252.
Volkheimer, W., Scafati, L., Melendi, D.L., 2007. Palynology of a Danian warm climatic wetland in central northern Patagonia, Argentina. Rev. Esp. Micropaleontol. 39, 117–134.
Yamada, T., Kato, M., 2002. *Regnellites nagashimae* gen. et sp. nov., the oldest macrofossil of Marsileaceae, from the Upper Jurassic to Lower Cretaceous of western Japan. Int. J. Plant Sci. 163, 715–723.
Yi, S., Batten, D.J., 2002. Palynology of Upper Cretaceous (uppermost Campanian–Maastrichtian) deposits in the South Yellow Sea Basin, offshore Korea. Cretac. Res. 23, 687–706.
Zavialova, N., Batten, D.J., 2018. Species of the water-fern megaspore genus *Molaspora* from a Cenomanian deposit in western France: occurrence, sporoderm ultrastructure and evolutionary relationships. Grana 57, 325–344.