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The South American and Antarctic Peninsula fossil record of Salviniales (water ferns): Its implication for understanding their evolution and past distribution

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ABSTRACT

We compiled the fossil record of the heterosporous water ferns (Salviniales) including macro- and microfossils from South America and the Antarctic Peninsula. Both extant families, Marsileaceae and Salviniaceae, are well represented and several fossil spore genera that cannot be placed within the extant families are included as Incertae sedis. Marsileaceae is first recorded in the Middle to Late Jurassic. Incertae sedis genera are recorded for first time in the Early Cretaceous while Salviniaceae in the Late Cretaceous. Two diversity spikes are recognized: one spanned the Aptian–Albian (Early Cretaceous) and is linked to an increase in species diversity within Marsileaceae; and the other occurred during the Campanian–Maastrichtian (Late Cretaceous) and it is associated with the diversification at generic level of the entire Salviniales. Two decreases in diversity are recognized: one during the Cenomanian–Santonian and affected Marsileaceae at specific level but not its generic diversity, and the second is related to the Cretaceous–Paleogene mass extinction and affected all Salviniales at generic and specific levels. From the Paleocene onwards there is a steady decline in the fossil record of the group, with most remains belonging to the extant genera. This study suggests that Southern Hemisphere aquatic ferns underwent a sharp radiation during the Late Cretaceous and a deep decline in the Paleocene that parallels that occurred in the Northern Hemisphere. Probably, the temporal co-occurrence of geological and climate events and the availability of suitable lineages promoted the evolutionary changes of the water ferns in the studied area, including the high diversification and distribution in the Cretaceous and the subsequent post-Maastrichtian decline.

1. Introduction

Heterosporous water ferns constitute a monophyletic clade that includes two extant families, Marsileaceae Mirbel and Salviniaceae Martinov, within the order Salviniales Link (Smith et al., 2006; PPG I, 2016). Marsileaceae has three extant genera: *Marsilea* L. (~50 species) distributed in tropical to temperate regions worldwide and in South America from northern Venezuela to central Argentina; *Regnellidium* Lindm. with one species restricted to a small region of southern Brazil and adjacent territories of Paraguay and Argentina; and *Pilularia* L. (~5 species) with a disjunct distribution in both hemispheres and specifically in South America from northern Venezuela to central Argentina and Chile (Tryon and Tryon, 1982; Tryon and Lugardon, 1991; Pryer, 1999; Nagalingum et al., 2006). Salviniaceae comprises two extant genera: *Azolla* Lam. with (~7 species) distributed in temperate to tropical regions worldwide, in South America from northern Venezuela to southern Chile and the Falkland/Malvinas Islands; and *Salvinia* Ség. (~10 species) distributed in temperate to tropical zones worldwide, in South America from northern Venezuela to central Argentina (Tryon and Tryon, 1982; Tryon and Lugardon, 1991; Nagalingum et al., 2006).

The macro- and microfossil record of Marsileaceae is widespread, with a large stratigraphic and geographic distribution, occurring worldwide from the Late Jurassic–Early Cretaceous (Yamada and Kato, 2002) or maybe Late Triassic (Sun et al., 2014) to the Present (Collinson, 1991, 2001; Lupia et al., 2000; Estrada-Ruiz et al., 2018; Hermsen, 2019). The fossil record of Salviniaceae starts latter, in the Late Cretaceous, and it is mostly based on dispersed megaspores and microspore massulae probably because their sporophytes are extremely fragile and therefore less likely to preserve (Weber, 1973; Hoffman and Stockey, 1994; Collinson et al., 2013; Hermsen et al., 2019). Fossils that can be assigned to modern *Marsilea* (Hermsen, 2019), *Regnellidium* (Cúneo et al., 2013), *Azolla* (Hermsen et al., 2019) and *Salvinia* (Weber, 1973; Schrank, 1994) are known from the Late Cretaceous. During the Late Cretaceous, the modern genera existed alongside several fossil genera, most of them corresponding only to dispersed megaspores (Batten and Kovach, 1990; Collinson, 1991, 2001). Therefore, the finding of in situ spores from

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fertile whole plants is essential for understanding the phylogeny, diversification, and extinction patterns in aquatic ferns (Collinson, 1991; Rothwell and Stockey, 1994; Hermsen et al., 2019).

Kovach and Batten (1989) and Batten and Kovach (1990) published a first compilation of salvinialean fossil megaspores that was included as part of a catalog of Mesozoic and Tertiary megaspores genera and species worldwide. Later on, other authors have gathered information on macro- and microfossil records related to Salviniales or to a particular group within this clade (e.g., Collinson, 2001; Nandi and Chattopadhyay, 2003; Vajda and McLoughlin, 2005; Kutluk et al., 2011; Batten et al., 2016; Pérez-Consuegra et al., 2017; Hermsen, 2019; among others).

Interestingly, even though the salvinialean fossil record is quite abundant and it has been treated abundantly in the literature, there is not a comprehensive compilation of the complete fossil record of Salviniales worldwide. In this contribution, we present an exhaustive bibliographical review of the salvinialean fossil record from South America and the Antarctic Peninsula while providing key information on the austral paleogeographic and paleoenvironmental history of the group as a starting point. Furthermore, this compendium is crucial to test if a diversification/decline scenario similar to the one observed at the Northern Hemisphere had occurred in the Southern Hemisphere at the same time.

2. Materials and methods

Records in this contribution include those published in scientific journals, books, and special publications while abstracts and unpublished theses were included when they are of exceptional interest. The information was gathered in an Excel file that is provided as supplementary material (Appendix A). For the quantitative and qualitative analyzes and to better visualize the changes through geological time, the record was grouped into arbitrary time intervals as follows: Callovian–Tithonian; Berriasian–Barremian; Aptian–Albian; Cenomanian–Santonian; Campanian–Maastrichtian; Paleocene–Oligocene; Miocene–Pliocene; and Pleistocene–Holocene. A single file/entry (one record) corresponds to a taxonomic unit from a single stratigraphic unit or informal strata. However, when a record spans more than one of these time intervals (e.g., Maastrichtian–Paleocene), it is registered as two files/entries to avoid underrepresentation in the diversity analyses (e.g., see below *Azolla boliviensis*). A taxonomic unit can be a formal fossil species (e.g., *Mirasolita irupensis*, in Hermsen et al., 2014), a taxon in open nomenclature (e.g., *Azolla* sp., in Quattrocchio et al., 2005) or an informal name (e.g., 'Marsileaceae', in Monje Dussán et al., 2016). The taxonomy and ages of the fossils are updated based on the latest publications. Efforts are focused in pre-Quaternary records.

Fossil records were organized into three groups: Marsileaceae, Salviniaceae, and Incertae sedis (which includes those macro- and microfossils species whose affinity with either of the two extant families has not been clearly demonstrated). Those fossil spore species for which the mega- and microspore are known to be produced by the same parent plant were considered as a single species in the diversity analyzes (e.g., *Molaspora lobata*/*Crybelosporites pannuceus*, in Lupia et al., 2000; *Molaspora reticulata*/*Gabonisporis cristata*, in Aulenback, 2009; *Arcellites santacrucensis*/*Crybelosporites australis*, in Villar de Seoane and Archangelsky, 2008). We are aware that different fossil dispersed spores could have been produced by the same parent plant but because the parental origin cannot be confirmed they are considered as different genera/species. Two examples of this are *Lugiomarsiglia aquatica* (sporocarps) and *Mirasolita irupensis* (leaves) from the Maastrichtian of Argentina and macrofossils of *Regnellidium thomas-taylorii* that were found associated with the fossil spores of *Molaspora lobata* and *Crybelosporites pannuceus* (Cúneo et al., 2013; Hermsen et al., 2014).

Figs. 1–3 were plotted with the Palaeontological Statistics program (PAST; Hammer et al., 2009) and edited using Adobe Photoshop CS6 (Adobe, San José, California, USA). To analyze the role that continental drift and the paleoenvironments could have had in the distribution and diversity of Salviniales, its fossil record was plotted on paleogeographic reconstructions of different geologic times (Figs. 4 and 5). For the paleogeographic reconstructions we used the PALEOMAP PaleoAtlas for GPlates (Scotese, 2016). Figs. 6 and 7 show the stratigraphic ranges of the genera and species, respectively, for South America and the Antarctic Peninsula listed in Appendix A.

	Marsileaceae	Salviniaceae	Incertae sedis
Callovian - Tithonian	2	0	0
Berriasian - Barremian	2	0	0
Aptian - Albian	78	0	11
Cenomanian - Santonian	21	0	14
Campanian - Maastrichtian	44	26	61
Paleocene - Oligocene	9	18	8
Miocene - Pliocene	0	21	0
Pleistocene - Holocene	1	8	0

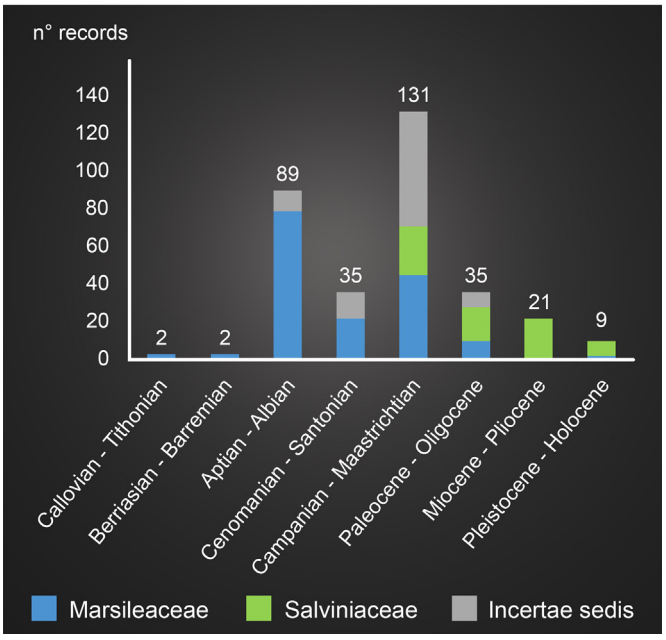

Fig. 1. Number of records through time. The numbers on the bars correspond to the total of records for each interval.

3. Results

A data list consisting of 324 records, including 16 macrofossils (sporophytes, leaves, and reproductive structures) and 308 microfossils (megaspores and microspores/microspore massulae) referred to the heterosporous water ferns from South America and the Antarctic Peninsula was made (Supplementary material, Appendix A).

An annotated alphabetical list of the 63 macro- and microfossil species considered is provided below (*note:* the number in parentheses is used as a reference for Figs. 4, 5, and 7; for those fossils that were not identified at the species level, a letter in parentheses is used as reference for Figs. 4 and 5).

3.1. Macrofossil record

3.1.1. Family Marsileaceae

(1) *Lugiomarsiglia aquatica* Gandolfo, Hermsen & Cúneo: sporocarps from the Maastrichtian of Patagonia, Argentina (Hermsen et al., 2014).

(2) *Mendozaphyllum loncochense* Puebla, Prámparo & Gandolfo: plant with rhizome, roots, and leaves from the Campanian–Maastrichtian of western Argentina (Puebla et al., 2014).

	Marsileaceae	Salviniaceae	Incertae sedis
Callovian - Tithonian	1	0	0
Berriasian - Barremian	1	0	0
Aptian - Albian	2	0	3
Cenomanian - Santonian	3	0	3
Campanian - Maastrichtian	8	1	7
Paleocene - Oligocene	2	2	2
Miocene - Pliocene	0	2	0
Pleistocene - Holocene	1	2	0

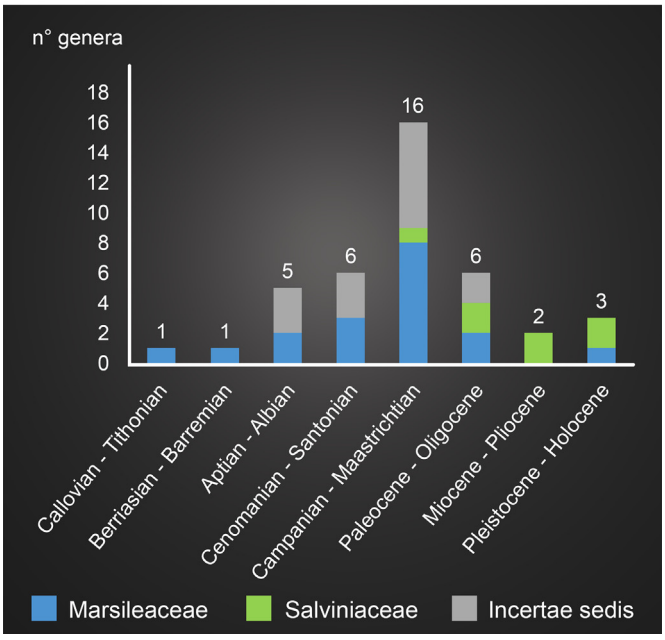

Fig. 2. Number of genera through time. The numbers on the bars correspond to the total of genera for each interval.

	Marsileaceae	Salviniaceae	Incertae sedis
Callovian - Tithonian	2	0	0
Berriasian - Barremian	1	0	0
Aptian - Albian	18	0	4
Cenomanian - Santonian	7	0	5
Campanian - Maastrichtian	9	7	15
Paleocene - Oligocene	3	7	3
Miocene - Pliocene	0	3	0
Pleistocene - Holocene	1	2	0

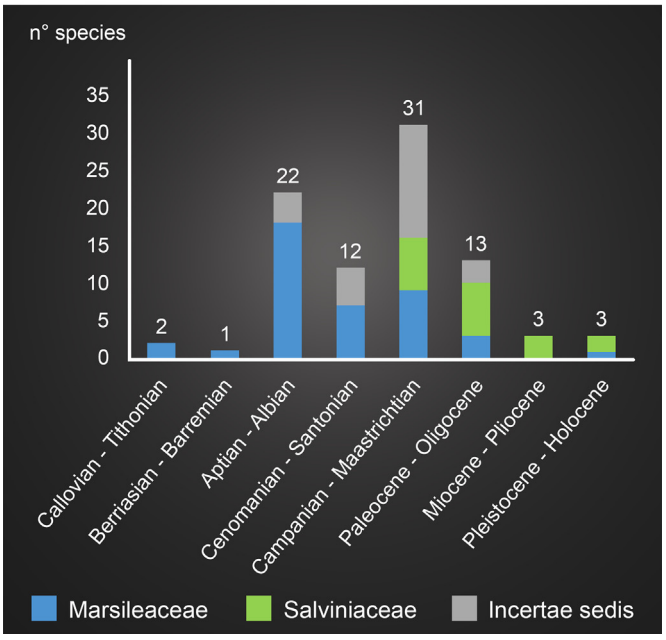

Fig. 3. Number of species through time. Only formal fossil species and those with open nomenclature but described in detail as differentiated species, were included in this figure. Those species for which the micro- and megaspore were recorded attached and confirmed to belonging to the same species were considered as individual species when they were found in the same sediments (see Appendix A). The numbers on the bars correspond to the total of species for each interval.

(3) *Mirasolita irupensis* Hermsen, Gandolfo & Cúneo: leaves from the Maastrichtian of Patagonia, Argentina (Hermsen et al., 2014).

(4) *Regnellidium thomas-taylorii* Cúneo, Gandolfo & Hermsen: plant with rhizome, roots, leaves and sporocarps from the Maastrichtian of Patagonia, Argentina (Cúneo et al., 2013).

(5) Marsileaceae: leaves from the Aptian of Colombia (Monje Dussán et al., 2016).

(6) Marsileaceae: leaves from the Albian of Alexander Island, Antarctic Peninsula (Nagalingum, 2007). Described as *Marsileaceaephyllum lobatum* Nagalingum and later referred to a fossil of uncertain affinity within Marsileaceae in Hermsen et al. (2014). The specimens described as *Marsileaceaephyllum* sp. B by Nagalingum (2007) are here considered as the same fossil taxon because, as indicated by the author, it is possible that the two species represent two morphological forms of a single species. See comments in Hermsen (2019).

(7) Marsileaceae: leaves and leaflets from the Maastrichtian of Patagonia, Argentina (Vallati et al., 2017). Described as *Marsileaceaephyllum* sp. and later referred to a fossil of uncertain affinity within Marsileaceae in Hermsen (2019).

3.1.2. Family Salviniaceae

(8) *Azolla coloniensis* De Benedetti & Zamaloa emend. Hermsen et al.: plant with roots, leaves and reproductive structures (including megaspores and microspore massulae) from the Maastrichtian–Danian of Patagonia, Argentina (De Benedetti et al., 2018; Hermsen et al., 2019; Clyde et al., 2021).

(9) *Azolla keuja* Hermsen et al.: plant with roots, leaves and reproductive structures (including megaspores and microspore massulae) from the Danian of Patagonia, Argentina (Hermsen et al., 2019).

(10) *Salvinia bogotensis* Cuervo & Pérez: plant with floating and submerged leaves from the late Paleocene of Colombia (Pérez-Consuegra et al., 2017).

(11) *Salvinia graui* Herbst & Anzótegui: leaves from the Miocene of northern Argentina (Herbst et al., 1987).

(12) *Salvinia magdalenensis* Cuervo & Pérez: plant with floating and submerged leaves from the late Eocene of Colombia (Pérez-Consuegra et al., 2017).

(13) *Salvinia* sp. cf. *S. minima* Baker: leaves from the Miocene (Herbst et al., 1987) and Holocene (Contreras and Robledo, 2021) of northern Argentina.

(14) *Salvinia* sp. 1: plant with floating leaves from the late Eocene of Colombia (Pérez-Consuegra et al., 2017).

(15) *Salvinia* sp. 2: plant with floating and submerged leaves from the middle to late Paleocene of Colombia (Pérez-Consuegra et al., 2017).

3.2. Microfossil record

3.2.1. Family Marsileaceae

(16) *Arcellites disciformis* Miner emend. Ellis & Tschudy: megaspore. Aptian–Cenomanian of Patagonia, Argentina (Baldoni and Batten, 1991; Santamarina et al., 2018, 2020). 2 records.

(17) *Arcellites humilis* Villar de Seoane & Archangelsky: megaspore. Albian–Cenomanian of Patagonia, Argentina (Villar de Seoane and Archangelsky, 2008, 2013). 3 records.

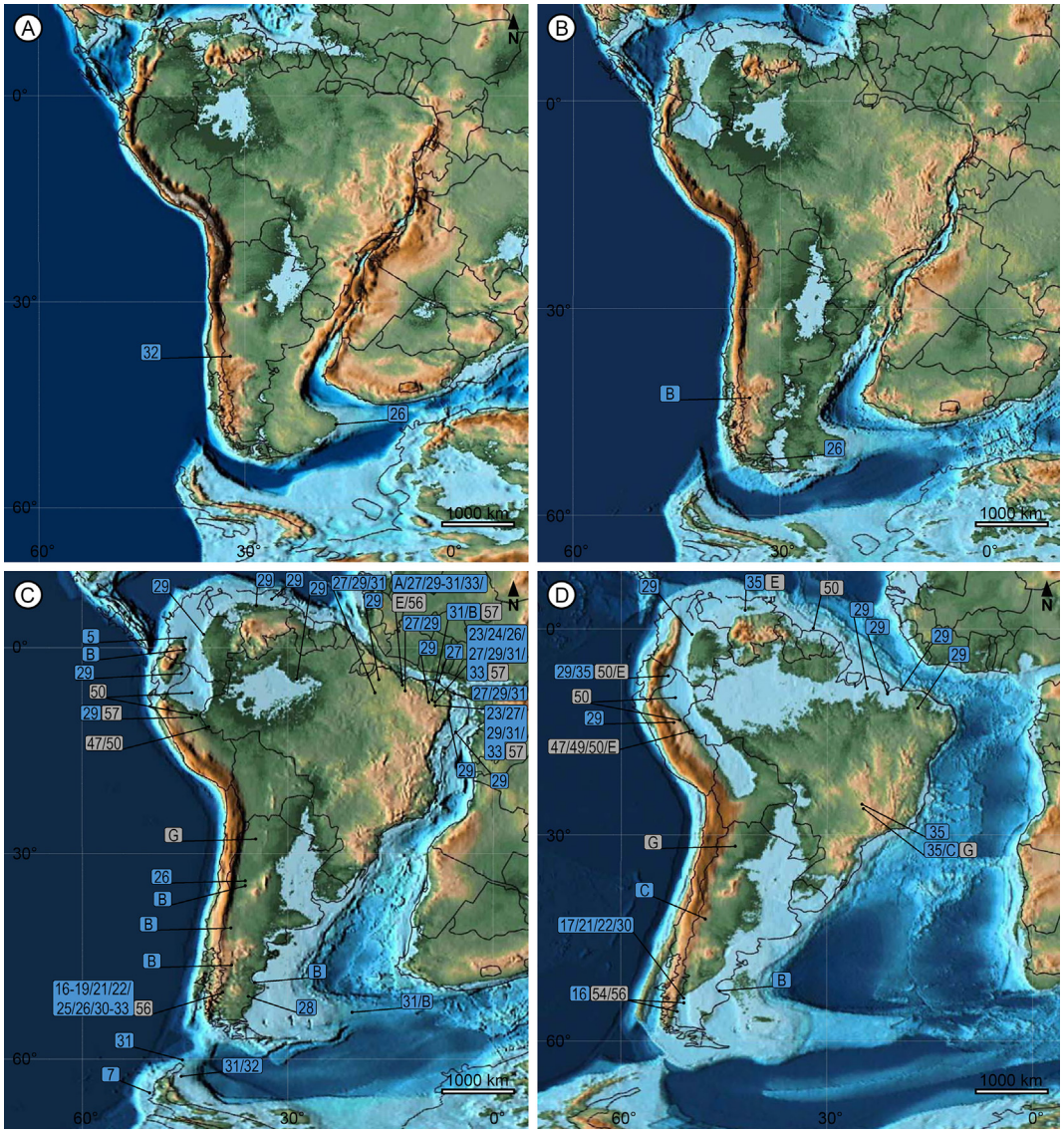

Fig. 4. Paleogeographic reconstructions showing records of Salviniales, numbers and letters correspond to those of the Results section. A. Middle to Late Jurassic (Map of 145 Ma of Scotese, 2016). B. Berriasian–Barremian (Map of 132 Ma of Scotese, 2016). C. Aptian–Albian (Map of 113 Ma of Scotese, 2016). D. Cenomanian–Santonian (Map of 90 Ma of Scotese, 2016). Some records occurring in the same geographic region have been combined. The color of the rectangles corresponds to blue: Marsileaceae; green: Salviniaceae; and gray: Incertae sedis.

(18) *Arcellites* sp. cf. *A. nudus* (Cookson & Dettmann) Potter: megaspore. Aptian–Albian of Patagonia, Argentina (Del Fueyo et al., 2007). 1 record.

(19) *Arcellites pentagonalis* Villar de Seoane & Archangelsky: megaspore. Albian of Patagonia, Argentina (Villar de Seoane and Archangelsky, 2008). 1 record.

(20) *Arcellites* sp. cf. *A. reticulatus* Potter: megaspore. Campanian–Maastrichtian of Patagonia, Argentina (Baldoni and Batten, 1997). 1 record.

(21) *Arcellites santacrucensis* Baldoni: megaspore. Aptian–Cenomanian of Patagonia, Argentina (Baldoni, 1987; Baldoni and Taylor, 1988; Batten et al., 1996; Villar de Seoane and Archangelsky, 2008). 3 records.

(22) *Arcellites* sp. A: megaspore. Aptian–Cenomanian of Patagonia, Argentina (Villar de Seoane and Archangelsky, 2008). 2 records.

(23) *Arcellites* sp. 1: megaspore. Aptian–Albian of northeastern Brazil (de Lima, 1978, 1979). 2 records.

(24) *Arcellites* sp. 2: megaspore. Aptian–Albian of northeastern Brazil (de Lima, 1979). 1 record.

(A) *Arcellites* spp.: megaspores. Aptian of northeastern Brazil (Ferreira et al., 2020) and Campanian–Maastrichtian of Venezuela (Fasola and Paredes de Ramos, 1991). 2 records.

(25) *Crybelosporites australis* Archangelsky & Llorens: microspore. Aptian–Albian of Patagonia, Argentina (Archangelsky and Llorens, 2005; Villar de Seoane and Archangelsky, 2008). Found among the appendages of *Arcellites santacrucensis*. 1 record.

(26) *Crybelosporites berberioides* Burger: microspore. Late Jurassic–Early Cretaceous. Sparsely distributed from the Falkland Plateau (Kotova, 1983) and southern Argentina (Cornú, 1986; del Fueyo et al., 2007) to northeastern Brazil (de Lima, 1979). 6 records.

(27) *Crybelosporites brennerii* Playford: microspore. Aptian–Albian of northeastern Brazil (de Lima, 1978, 1979, 1982; Ferreira et al., 2020; among others). 7 records.

(28) *Crybelosporites corrugatus* Perez Loinaze & Llorens: microspore. Aptian of Patagonia, Argentina (Perez Loinaze and Llorens, 2018). 1 record.

(29) *Crybelosporites pannuceus* (Brenner) Srivastava: microspore. Widely recorded from Aptian to Danian. Most of them from the

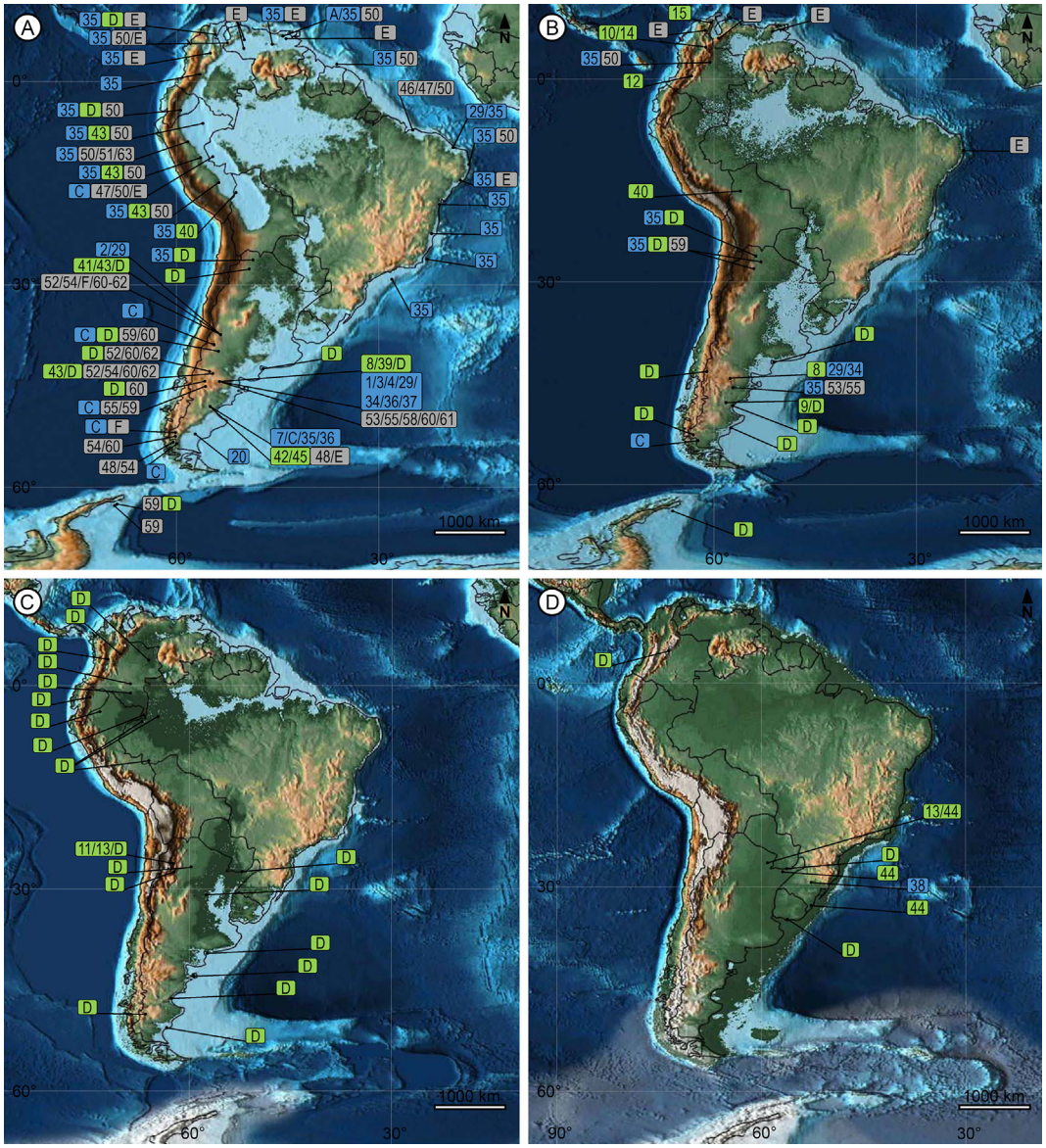

Fig. 5. Paleogeographic reconstructions showing records of Salviniales, numbers and letters correspond to those of the Results section. A. Campanian–Maastrichtian (Map of 76 Ma of Scotese, 2016). B. Paleocene–Oligocene (Map of 56 Ma of Scotese, 2016). C. Miocene–Pliocene (Map of 13 Ma of Scotese, 2016). D. Pleistocene–Holocene (Map of 1,8 Ma of Scotese, 2016). Some records occurring in the same geographic region have been combined. The color of the rectangles corresponds to blue: Marsileaceae; green: Salviniaceae; and gray: Incertae sedis.

Aptian–Cenomanian of northern South America (Brenner, 1968; Herngreen and Duenas Jimenez, 1990; Jaillard et al., 1995, 1997; Helenes and Somoza, 1999; among others). 33 records.

(30) *Crybelosporites punctatus* Dettmann: microspore. Aptian of northeastern Brazil (Ferreira et al., 2020) and Aptian–Cenomanian of southern Argentina (Medina et al., 2008; Villar de Seoane and Archangelsky, 2008; Archangelsky et al., 2012). 5 records.

(31) *Crybelosporites striatus* (Cookson & Dettmann) Dettmann: microspore. Sparsely recorded from the Aptian of northeastern Brazil (Batten, 2007; Ferreira et al., 2020; among others). One record from the Albian of the Falkland Plateau (Kotova, 1983) and the Aptian–Albian of southern Argentina (Archangelsky et al., 2012), and two records from the Aptian–Albian of the Antarctic Peninsula (Dettmann and Thomson, 1987; Hathway et al., 1999). 10 records.

(32) *Crybelosporites stylosus* Dettmann: microspore. Callovian (middle Jurassic) and Albian of southern Argentina (Scafati and Morbelli, 1984; Archangelsky et al., 2008), and the Aptian–Albian of the Antarctic Peninsula (Dettmann and Thomson, 1987; Riding et al., 1998). 5 records.

(33) *Crybelosporites truncatus* de Lima: microspore. Aptian–Albian of northeastern Brazil (de Lima, 1978, 1979; Ferreira et al., 2016, 2020) and southern Argentina (Baldoni and Batten, 1991). 4 records.

(B) *Crybelosporites* spp. (e.g., *C.* sp., *C.* sp.1, *C.* sp. A, and *C.* sp. B): microspores. Hauterivian–Maastrichtian of South America and the Falkland Plateau (Archangelsky and Seiler, 1980; Ludwig et al., 1983; Prámparo, 1989; Prössl and Vergara Streinesberger, 1993; among others). 13 records.

(34) *Gabonisporis cristata* (Stanley) Sweet: microspore. Maastrichtian–Danian of Patagonia, Argentina (Clyde et al., 2021; De Benedetti et al., 2021). 2 records.

(35) *Gabonisporis vigourouxii* Boltenhagen: microspore. Widely recorded from Late Cretaceous deposits, particularly from the Campanian–Maastrichtian interval of northern South America (Ashraf and Stinnesbeck, 1988; Fasola and Paredes de Ramos, 1991; Jaillard et al., 1995, 1997; Vajda-Santivanez, 1999; Arai and Dias-Brito, 2018; among others). Also sparsely recorded from the Maastrichtian–Danian of southern Argentina (Volkheimer et al., 2007; Vallati et al., 2016,

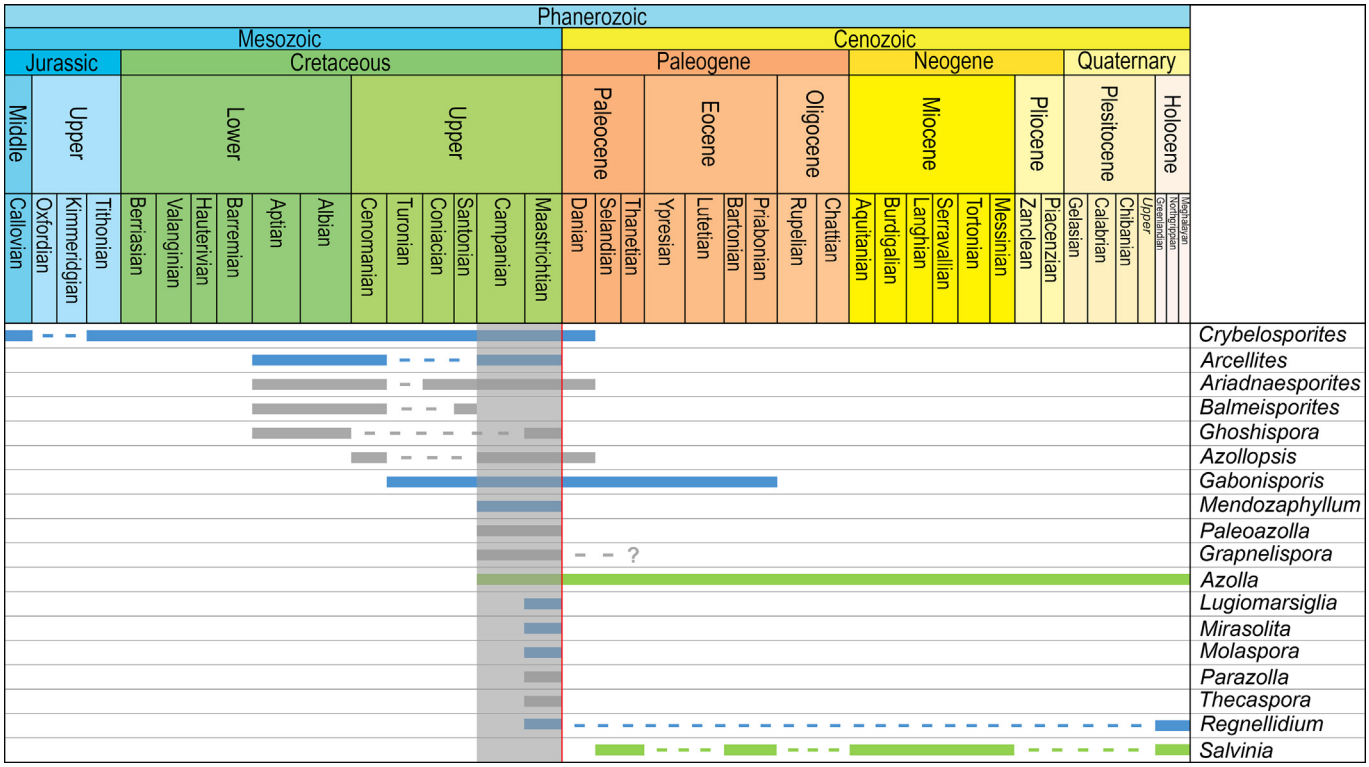

Fig. 6. Stratigraphic range of the Salviniales fossil genera from South America and the Antarctic Peninsula. The genera are arranged in order of first appearance. The shaded area indicates a time of high diversity. The dashed lines indicate gaps in the fossil record of the genera. The red line indicates the K–Pg boundary. The color of the bars corresponds to blue: Marsileaceae; green: Salviniaceae; and gray: Incertae sedis.

2017), Paleocene of Colombia (Jaramillo et al., 2011), and Paleocene to Eocene of northern Argentina (Quattrocchio, 1978; Quattrocchio et al., 1997; Narváez and Volkheimer, 2011; among others). 33 records.

(C) *Gabonisporis* spp. (described as *G.* sp. and *G.* sp. 1): microspores. Santonian to Danian deposits of Brazil to southern Argentina (Arai and Dias-Brito, 2018; Volkheimer et al., 2006; Vallati, 2010; Povilauskas, 2017; among others). 8 records.

(36) *Molaspora lobata* (Dijkstra) Hall: megaspore. Maastrichtian of Patagonia, Argentina (Cúneo et al., 2013, 2014; Hermsen et al., 2014; Vallati et al., 2017). 2 records.

(37) *Molaspora reticulata* Campbell and Untergasser: megaspore. Maastrichtian of Patagonia, Argentina (De Benedetti et al., 2021). 1 record.

(38) *Regnellidium diphyllum* Lindman: extant. Recorded as dispersed microspores in Holocene sediments of southern Brazil (Leal and Lorscheitter, 2006). 1 record.

3.2.2. Family Salviniaceae

(39) *Azolla andreisii* De Benedetti & Zamaloa: megaspore. Maastrichtian of Patagonia, Argentina (De Benedetti et al., 2021). 1 record.

(40) *Azolla boliviensis* Vajda & McLoughlin: megaspore and microspore massulae. Maastrichtian–Danian of Bolivia (Vajda-Santivanez, 1999; Vajda and McLoughlin, 2005). 2 records.

(41) *Azolla circinata* Oltz & Hall: microspore massulae. Campanian–Maastrichtian of western Argentina (Puebla et al., 2014). 1 record.

(42) *Azolla colhuehuapensis* Vallati et al.: megaspore and microspore massulae. Maastrichtian of Patagonia, Argentina (Vallati et al., 2017). 1 record.

(43) *Azolla cretacea* Stanley: microspore massulae. Maastrichtian of Perú (Jaillard et al., 1995), and Campanian–Maastrichtian of northern Patagonia, Argentina (Papú and Sepúlveda, 1995; Papú, 2002, 2006). However, all these records should be considered as *Azolla* sp., and the assignment of isolated microspore massulae to the species level should be avoided. 4 records.

(44) *Azolla filiculoides* Lamarck: extant. Recorded as dispersed microspore massulae in Holocene sediments of southern Brazil (Medeanic et al., 2000, 2001, 2006; Leal and Lorscheitter, 2006; Macedo et al., 2007) and northern Argentina (Contreras and Robledo, 2021). 3 records.

(45) *Azolla* sp. 1: megaspore. Maastrichtian of Patagonia, Argentina (Vallati et al., 2017). 1 record.

(D) *Azolla* spp.: microspore massulae. Widely recorded from Campanian to Holocene deposits of South America (Papú, 1990; Guler et al., 2001; Barreda et al., 2009; de Oliveira Medeiros et al., 2011; among others). Two records from the Maastrichtian–Danian of the Antarctic Peninsula (Baldoni and Barreda, 1986; Askin, 1989, 1990; Bowman et al., 2014; Scasso et al., 2020). 50 records.

3.2.3. Family Incertae sedis

(46) *Ariadnaesporites cristatus* Tschudy; megaspore/microspore. Campanian of northeastern Brazil (Lima, 1974). 1 record.

(47) *Ariadnaesporites longiprocessum* (Hills and Jensen) Hills: megaspore/microspore. Albian–Maastrichtian of Brazil (Lima, 1974; Haag, 2019). 5 records.

(48) *Ariadnaesporites micromedusus* Stough: megaspore/microspore. Campanian–Maastrichtian of southern Argentina and Chile (Stough, 1968; Vallati et al., 2016). 2 records.

(49) *Ariadnaesporites potoniei* Kedves: megaspore/microspore. Cenomanian of western Brazil (Haag, 2019). 1 record.

(50) *Ariadnaesporites spinosus* (Elsik) Hills: megaspore/microspore. Widely recorded from the Albian–Maastrichtian of northern South America (Elsik, 1966; Lima, 1974; Belsky et al., 1975; Fasola and Paredes de Ramos, 1991; Jaillard et al., 1995, 1997; de Oliveira Alves et al., 2019; among others). Only one record from the early Paleocene of Colombia (Jaramillo et al., 2011). 19 records.

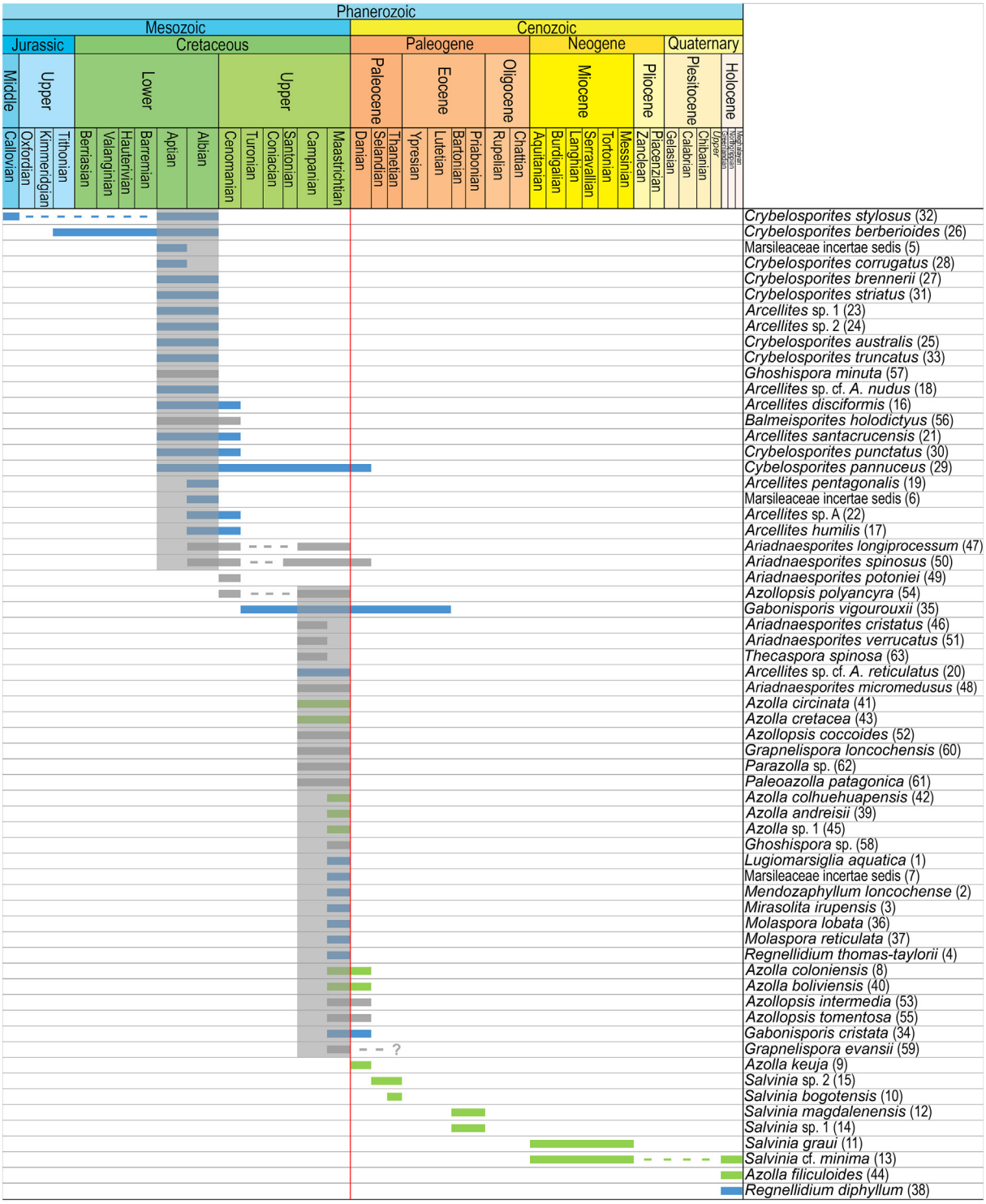

Fig. 7. Stratigraphic range of the Salviniales fossil species from South America and the Antarctic Peninsula. The species are arranged in order of first appearance. The number in parentheses correspond to those used in the text. The shaded areas indicate times of high diversity. The dashed lines indicate gaps in the fossil record of the species. The red line indicates the K–Pg boundary. The color of the bars corresponds to blue: Marsileaceae; green: Salviniaceae; and gray: Incertae sedis.

(51) *Ariadnaesporites verrucatus* (Elsik) Hills: megaspore/microspore. Campanian of Perú (Elsik, 1966). 1 record.

(E) *Ariadnaesporites* spp.: megaspore/microspore. Aptian to Danian deposits (Albertão et al., 1994; Jaillard et al., 1997; de la Parra, 2009; Ferreira et al., 2020; among others). 18 records.

(52) *Azollopsis coccoides* Hall emend. Sweet & Hills: microspore massulae. Campanian–Maastrichtian of southern Argentina (Papú et al., 1988; Papú and Sepúlveda, 1995). 3 records.

(53) *Azollopsis intermedia* Sweet & Hills: megaspore and microspore massulae. Maastrichtian–Danian of southern Argentina (Volkheimer et al., 2007; Scafati et al., 2009; De Benedetti et al., 2021). 2 records.

(54) *Azollopsis polyancyra* (Stough) Hall: microspore massulae. Cenomanian–Maastrichtian of southern Argentina and Chile (Stough, 1968; Papú and Sepúlveda, 1995; Papú, 2002; Marenssi et al., 2004). 5 records.

(55) *Azollopsis tomentosa* Hall: megaspore and microspore massulae. Maastrichtian–Danian of southern Argentina (Volkheimer et al., 2007; Scafati et al., 2009; Barreda et al., 2012; De Benedetti et al., 2021). 3 records.

(F) *Azollopsis* spp.: microspore massulae. Maastrichtian of southern Argentina (Papú, 2006; Santamarina et al., 2020). 3 records.

(56) *Balmeisporites holodictyus* Cookson & Dettmann: megaspore. Aptian of northeastern Brazil (Ferreira et al., 2020) and Aptian–Cenomanian of southern Argentina (Villar de Seoane and Archangelsky, 2008; Santamarina et al., 2018, 2020). The genus *Balmeisporites* has been traditionally related to the Marsileaceae due to the presence of an acrolamella and the structure of the wall. However, spores assignable to *B. holodictyus* were found inside the sporangia of *Heroleandra* Krassilov & Golovneva from the late Cretaceous of western Siberia (Krassilov and Golovneva, 2000). This peculiar fossil was placed in a new order of heterosporous plants (Krassilov and Golovneva, 2000). Therefore, *B. holodictyus* might not be related to the aquatic ferns, although it is here retained in Salviniales until more detailed studies clarify their taxonomic position. 3 records.

(G) *Balmeisporites* sp.: megaspore. Albian–Cenomanian of northern Argentina (Narváez et al., 2014). Late Santonian of southeastern Brazil (Arai and Dias-Brito, 2018). 3 records.

(57) *Ghoshispora minuta* (Brenner) Kutluk et al.: megaspore/microspore. Aptian–Albian of northeastern Brazil (de Lima, 1978, 1979; Batten, 2007). Albian of Perú (Brenner, 1968; Jaillard et al., 1995). 4 records.

(58) *Ghoshispora* sp.: megaspore/microspore. Maastrichtian of southern Argentina (De Benedetti et al., 2021). 1 record.

(59) *Grapnelispora evansii* Stover & Partridge: microspore massulae. Maastrichtian of southern Argentina (Papú et al., 1999; Palamarczuk and Gamerro, 1988; Barreda et al., 2012) and the Antarctic Peninsula (Baldoni and Barreda, 1986; Askin, 1990; Pirrie et al., 1997; Bowman et al., 2014; Scasso et al., 2020). One record from the Paleocene of northern Argentina (Quattrocchio et al., 1997, 2000; Narváez and Volkheimer, 2011). 5 records.

(60) *Grapnelispora loncochensis* Papú: microspore massulae. Campanian–Maastrichtian of southern Argentina (Papú, 1993, 1997; Marenssi et al., 2004; Vallati, 2010; Puebla et al., 2014; among others). 9 records.

(61) *Paleoazolla patagonica* Archangelsky et al. emend. De Benedetti & Zamaloa: megaspore and microspore massulae. Maastrichtian of Patagonia, Argentina (Archangelsky et al., 1999; Puebla et al., 2014; De Benedetti et al., 2020). 2 records.

(62) *Parazolla* sp.: microspore massulae. Campanian–Maastrichtian of southern Argentina (Papú et al., 1988; Papú, 2006). 3 records.

(63) *Thecaspora spinosa* Elsik: megaspore/microspore. Campanian of Perú (Elsik, 1966). 1 record.

3.2.4. The genus Hydrosporis Krutzsch

It is important to mention the genus *Hydrosporis* Krutzsch. It was created for trilete laevigate microspores with similar morphology to those produced by modern *Azolla* and *Salvinia* (Krutzsch, 1962). However, microspores of extant Salviniaceae are produced in massulae, and therefore, the relationship of the genus *Hydrosporis* to Salviniaceae is mostly based on the small size, spherical shape, and weak sculpture of the spores. This kind of spores can be found in the modern genera *Azolla* and *Salvinia*, but also in the massulae of several fossil genera such as *Azollopsis* and *Parazolla*. Records of this genus were incorporated at the end of the data list without a reference number and have not been considered in the diversity analyses.

(s/n) *Hydrosporis minor* da Silva-Caminha et al.: microspore. Late Oligocene–Pliocene of Brazil (da Silva-Caminha et al., 2010; Haag, 2019). 2 records.

(s/n) *Hydrosporis* sp.: microspore. Eocene–Oligocene of the Antarctic Peninsula (Stuchlik, 1981; Birkenmajer and Zastawniak, 1989). 1 record.

4. Discussion

4.1. Quantitative, qualitative and stratigraphic analyses

4.1.1. Number of records through time (Fig. 1)

The oldest record of water ferns corresponds to Marsileaceae and dates from the Middle Jurassic (Callovian) and the uppermost Jurassic (Tithonian). Only two other records of Marsileaceae were documented until the Barremian. Remarkably, the number of records jumped from 2 to 89 during the Aptian–Albian interval, most of them related to Marsileaceae and a few to salvinialean Incertae sedis. The number of records declines to 35 during the Cenomanian–Santonian interval, with 21 records of Marsileaceae and 14 of Incertae sedis; notably, 24 are from the Cenomanian and only 11 from the Turonian–Santonian interval.

It is in the Campanian–Maastrichtian interval that the fossil record of Salviniales reached its highest number reaching 131 records. Definitely, this is due to the appearance of the Salviniaceae with 26 records and a massive increase in number of records of salvinialean Incertae sedis microfossils (61 records). After a significant presence of Marsileaceae during the Aptian–Albian interval, its number declined from 78 to 21 in the early Late Cretaceous but it bounced to 44 records during the Campanian–Maastrichtian.

Clearly, the fossil record of Salviniales dropped in abundance after the K–Pg boundary, with only 35 records in the Paleocene–Oligocene interval, most of them from the early Paleocene (22 records). Marsileaceae and salvinialean Incertae sedis are restricted to a few mentions, 9 and 8 records respectively, while Salviniaceae is the most represented (18 records). During the Miocene–Pliocene interval 21 records were registered and all of them belonging to Salviniaceae. During the Pleistocene–Holocene interval, Salviniaceae comprises 8 records and Marsileaceae only 1.

This analysis demonstrates the presence of two well-defined intervals of high abundance of aquatic ferns in South America and the Antarctic Peninsula, one during the Aptian–Albian related to Marsileaceae and a second one during the Campanian–Maastrichtian comprising the entire salvinialean clade. From the Paleocene onwards, there is a steady decline in the number of fossil records.

4.1.2. Number of genera through time (Figs. 2 and 6)

As mentioned above, only Marsileaceae is recorded throughout the Callovian–Barremian interval, represented solely by *Crybelosporites*. In the Aptian–Albian several new spore genera are recorded; Marsileaceae is represented by *Crybelosporites* and *Arcellites* while the salvinialean Incertae sedis are represented by *Ariadnaesporites*, *Balmeisporites*, and *Ghoshispora*. During the Cenomanian–Santonian, Marsileaceae is represented by the genera *Crybelosporites*, *Arcellites,* and *Gabonisporis*, and the Incertae sedis by *Ariadnaesporites*, *Balmeisporites,* and *Azollopsis*. The number of genera increases remarkably during the Campanian–Maastrichtian interval. In addition to the previously mentioned spore fossil genera (excluding *Balmeisporites*), several others are first recorded including *Grapnelispora*, *Molaspora*, *Paleoazolla*, *Parazolla,* and *Thecaspora*. Macrofossil genera *Lugiomarsiglia*, *Mendozaphyllum*, *Mirasolita,* and the modern *Azolla* and *Regnellidium* are recorded in this interval as well.

The generic diversity of aquatic ferns conspicuously decreases after the K–Pg boundary. During the Paleocene–Oligocene, the Incertae sedis comprises only *Azollopsis* and *Ariadnaesporites*, whereas Marsileaceae is represented by *Crybelosporites* and *Gabonisporis* and Salviniaceae by *Azolla* and *Salvinia*. Intriguingly, the Incertae sedis genera are restricted to the early Paleocene, while only *Gabonisporis* is recorded in the Eocene. From then on, the fossil record is constrained to *Azolla*, *Salvinia,* and *Regnellidium*.

Definitely, these data reveal the existence of a period of high diversity at the generic level for the Salviniales during the Campanian–Maastrichtian followed by a quick and deep decline in the Paleocene.

4.1.3. Number of species through time (Figs. 3–5, and 7)

Middle Jurassic–Early Cretaceous (Fig. 4, A–C): The oldest records are related to Marsileaceae and correspond to *Crybelosporites stylosus* from the Middle Jurassic (Neuquén Basin, Argentina; Scafati and Morbelli, 1984), and *Crybelosporites berberioides* from the uppermost Jurassic (Falkland Plateau; Kotova, 1983). Only two other records of this genus (*C. berberioides* and *C.* sp.), both from southern Argentina, were documented until the Barremian (Archangelsky and Seiler, 1980; Cornú, 1986; Del Fueyo et al., 2007). Two *Crybelosporites* species were recorded from the Callovian to the Barremian, while nine *Crybelosporites* species (*C. australis*, *C. berberioides*, *C. brenneri*, *C. corrugatus*, *C. pannuceus*, *C. punctatus*, *C. striatus*, *C. stylosus*, and *C. truncatus*) and eight *Arcellites* species (*A. disciformis*, *A. humilis*, *A.* sp. cf. *A. nudus*, *A. pentagonalis*, *A. santacrucensis*, *A.* sp. A, *A.* sp. 1, and *A.* sp. 2) were registered from the Aptian–Albian. Furthermore, the oldest macrofossil records related to Salviniales correspond to leaves of Marsileaceae from the Aptian of Colombia (Monje Dussán et al., 2016) and the Albian of the Antarctic Peninsula (Nagalingum, 2007; Hermsen et al., 2014). The presence of these marsileaceous fossils in such distant regions indicates that the family was probably widely distributed in the region during the Early Cretaceous. The Incertae sedis species *Ariadnaesporites longiprocessum*, *A. spinosus*, *Balmeisporites holodictyus*, and *Ghoshispora minuta*, although scarcely, were also recorded during the Aptian–Albian. During the Aptian–Albian interval, Marsileaceae is widely represented in South America and the Antarctic Peninsula, while the salvinialean Incertae sedis are restricted to South America.

Twenty-two species comprising 89 records were registered in the Aptian–Albian suggesting that aquatic ferns were highly diverse during that time. A first spike in abundance and diversity at the species level is recognized for this time interval, which is mainly related to the Marsileaceae, and particularly to the widespread distribution of the *Crybelosporites* and *Arcellites* species.

Late Cretaceous (Fig. 4, D; Fig. 5, A): After a significant presence of Marsileaceae during the Aptian–Albian, the family declined in species diversity and abundance during the early Late Cretaceous. Several *Arcellites* and *Crybelosporites* species that were common in Aptian–Albian sediments disappeared in the Late Cretaceous. During the Cenomanian, *Crybelosporites* is represented only by *C. pannuceus* and *C. punctatus* and *Arcellites* by *A. disciformis*, *A. humilis*, *A. santacrucensis*, and *A.* sp. A. In addition, the salvinialean Incertae sedis are represented by *Ariadnaesporites longiprocessum*, *A. potoniei, A. spinosus*, *Balmeisporites holodictyus*, and *Azollopsis polyancyra*. Species diversity notably declined during the Turonian–Santonian, Marsileaceae is restricted to *C. pannuceus* and the first report of *Gabonisporis vigourouxii*, while the Incertae sedis are represented only by *A. spinosus*. During the early Late Cretaceous, water ferns are scarcely represented in South America, particularly during the Turonian–Santonian interval, and they are absent in the fossil record of the Antarctic Peninsula.

A total of 22 fossil species are recorded in the Aptian–Albian while only three species in the Turonian–Santonian. Although the fossil record largely decreases in abundance and species diversity, it was not affected at generic level. Most Aptian–Albian fossil spore genera have some gap in their record during the Turonian–Santonian interval (see Fig. 6), but they are again recorded in the Campanian–Maastrichtian (except *Balmeisporites*). This decline in the record could be related in part to sampling biases due to the few geological units of Turonian–Santonian age in South America.

The specific diversity and abundance of water ferns increases notably during the Campanian–Maastrichtian interval. Remarkably, Salviniaceae appeared and became widely distributed from northern Colombia to the Antarctic Peninsula, mostly represented by dispersed microspore massulae of *Azolla*. The oldest macrofossil record of Salviniaceae corresponds to *Azolla coloniensis* from the Maastrichtian of northern Argentinean Patagonia (Hermsen et al., 2019). Salviniaceae is represented by six *Azolla* fossil spore species (*A. andreisii*, *A. boliviensis*, *A. circinata*, *A. colhuehuapensis*, *A. cretacea*, and *A.* sp. 1). As previously mentioned, several salvinialean Incertae sedis fossil spore genera are first recorded at this time as well, represented by the species *Grapnelispora evansii*, *G. loncochensis*, *Paleoazolla patagonica*, *Parazolla* sp., and *Thecaspora spinosa*. The genus *Azollopsis,* recorded for first time in Cenomanian deposits, is represented by four species (*A. polyancyra*, *A. coccoides*, *A. intermedia* and *A. tomentosa*) showing an increase in abundance and diversity during this period. Furthermore, this pattern is also observed in other taxa such as *Ariadnaesporites* that is represented by five species (*A. longiprocessum*, *A. spinosus*, *A. cristatus*, *A. verrucatus,* and *A. micromedusus*). The macrofossil record of Marsileaceae also increases during the Campanian–Maastrichtian, represented by *Lugiomarsiglia aquatica*, *Mendozaphyllum loncochense*, *Mirasolita irupensis*, *Regnellidium thomas-taylorii*, and leaves of an unidentified Marsileaceae (Cúneo et al., 2013; Hermsen et al., 2014; Puebla et al., 2014; Vallati et al., 2017) while its microfossil record is supported by the presence of *Arcellites* sp. cf. *A. reticulatus*, *G. vigourouxii*, *Molaspora lobata*/*Crybelosporites pannuceus*, and *Molaspora reticulata*/*Gabonisporis cristata*. However, it is interesting to note that Marsileaceae never again reaches the levels of diversity achieved during the Early Cretaceous. This decrease in the diversity could be related to many factors, such as competition with better adapted taxa, the reduction of favorable habitats for this particular group, or it could be related to their ecology and life history, which simply provide limited opportunities for preservation (Hermsen, 2019). During the Campanian–Maastrichtian interval, Marsileaceae, Salviniaceae, and the Incertae sedis were widely distributed in South America, while only Salviniaceae (i.e., *Azolla* sp.) and the salvinialean Incertae sedis (i.e., *Grapnelispora evansii*) are recorded in the Antarctic Peninsula.

The fossil record of Salviniales in the region reaches its acme during the Campanian–Maastrichtian interval, with a total of 131 records, 16 genera, and 31 species recognized, including members of the Marsileaceae (9 species), Salviniaceae (7 species), and Incertae sedis (15 species).

Paleogene (Fig. 5, B): The fossil record of Salviniales strikingly declined in diversity after the K–Pg boundary. During the early Paleocene, Marsileaceae is represented by *Crybelosporites pannuceus*, *Gabonisporis cristata,* and *G. vigourouxii*, Salviniaceae by *Azolla boliviensis, A. coloniensis* and *A. keuja*, and the salvinialean Incertae sedis by *Ariadnaesporites spinosus*, *Azollopsis intermedia,* and *A. tomentosa*. The Antarctic Peninsula is devoid of water fern fossils from the middle Paleocene onwards. The last salvinialean record from the Antarctic Peninsula corresponds to microspore massulae of *Azolla* from the Danian of the Seymour/Marambio Island (Baldoni and Barreda, 1986; Askin, 1989; Scasso et al., 2020). During the middle Paleocene to late Eocene, Marsileaceae is represented only by *G. vigourouxii*, and Salviniaceae by *Salvinia* sp., *S. bogotensis*, and *S. magdalenensis*, and dispersed massulae of *Azolla* sp. Only dispersed massulae of *Azolla* sp. are recorded in Oligocene sediments. Interestingly, no new fossil genera are recorded during the Paleogene and the diversity of the pre-existing ones is drastically declined. Fossil spore genera correspond to a few mentions of *Ariadnaesporites*, *Azollopsis*, and *Crybelosporites* from the early Paleocene, while only *Gabonisporis* is recorded until the Eocene. Probably, these few records belong to the survivors of the K/Pg mass extinction.

Neogene–Quaternary (Fig. 5, C, D): Throughout the Miocene–Holocene interval, the fossil record comprises only modern genera, and most of them correspond to dispersed *Azolla* microspore massulae. Neogene macrofossils are restricted to the Miocene of Argentina, represented by *Salvinia graui* and *Salvinia* cf. *S. minima*. Only the extant *A. filiculoides*, *Salvinia* cf. *S. minima*, and *Regnellidium diphyllum* have been recorded from Holocene sediments (Leal and Lorscheitter, 2006; Fernández Pacella et al., 2011; Contreras and Robledo, 2021; among others).

4.1.4. Stratigraphic ranges (Figs. 6 and 7)

In South America and the Antarctic Peninsula, the fossil record started in the Callovian (late Middle Jurassic) with *Crybelosporites* which it is the only genus recorded until the Aptian (Early Cretaceous). During the Aptian four new fossil genera are first recorded, including

the Marsileaceae *Arcellites* (Aptian–Maastrichtian), and the Incertae sedis *Ariadnaesporites* (Aptian–Danian), *Balmeisporites* (Aptian–Santonian) and *Ghoshispora* (Aptian–Maastrichtian). At the beginning of the Late Cretaceous, *Azollopsis* (Cenomanian–Danian) and *Gabonisporis* (Turonian–Eocene) are first recorded. The majority of the genera are restricted to the Late Cretaceous, particularly to the Campanian–Maastrichtian interval, including *Grapnelispora*, *Lugiomarsiglia*, *Mendozaphyllum*, *Mirasolita*, *Molaspora*, *Paleoazolla*, *Parazolla*, and *Thecaspora*. Among the modern genera, *Azolla* has a continuous record from Campanian to Present; *Regnellidium* has a single record in Maastrichtian deposits and a large gap until the Holocene; and *Salvinia* has a discontinuous record from the Paleocene onwards (Fig. 6).

Most species span relatively short stratigraphic ranges restricted to two highly diverse time intervals, the Aptian–Albian and the Campanian–Maastrichtian (Fig. 7). *Crybelosporites stylosus*, *C. berberioides*, *C. pannuceus*, and *Gabonisporis vigourouxii*, all of them corresponding to widely distributed marsileaceous microspores, are the only exceptions that have wide stratigraphic ranges.

C. stylosus and *C. berberioides* are the only two species recorded from the Middle Jurassic to the Barremian, and they are also recorded in Aptian–Albian deposits. During the Aptian–Albian, several species of *Crybelosporites* and *Arcellites* are recorded, along with *Ariadnaesporites spinosus*, *Balmeisporites holodictyus*, and *Ghoshispora minuta*. Some of these species extend their stratigraphic ranges to the Cenomanian, while only *C. pannuceus*, *Ariadnaesporites longiprocessum*, and *A. spinosus* are registered until the Maastrichtian or Danian. During the Turonian–Santonian, most of the Aptian–Albian species disappeared and only a few species including *Crybelosporites pannuceus*, *Ariadnaesporites spinosus*, and *Gabonisporis vigourouxii* are recorded.

The Campanian–Maastrichtian interval is characterized by the first and last occurrences of numerous fossil spore genera (i.e., *Grapnelispora*, *Molaspora*, *Paleoazolla*, *Parazolla* and *Thecaspora*) and species (e.g., *Azolla colhuehuapensis*, *Grapnelispora loncochensis*, *Molaspora reticulata* and *Paleoazolla patagonica*), and several macrofossil species (e.g., *Mendozaphyllum loncochense*, *Mirasolita irupensis,* and *Regnellidium thomas-taylorii*). The highest diversity in the evolution of aquatic ferns is reached during this time interval. Remarkably, several fossil species such as *Ariadnaesporites spinosus*, *Azolla boliviensis*, *A. coloniensis*, *Azollopsis intermedia*, *A. tomentosa*, *Crybelosporites pannuceus*, and *Gabonisporis cristata* crossed the K–Pg boundary and are found in the early Paleocene while *Gabonisporis vigourouxii* is the only one recorded until the Eocene. From then on, diversity declines markedly, and the few fossil species recorded are related to the modern genera.

4.2. Paleogeography and paleoenvironments

For assessing the role that the paleoenvironments played on the distribution and diversity of Salviniales, their fossil record was plotted onto paleogeographic reconstructions centered on South America and Antarctic Peninsula for different geologic times (Figs. 4 and 5).

Middle–Late Jurassic: This time interval is characterized by the onset of the breakup of Gondwana and the intensification of rifting (Nürnberg and Müller, 1991). South American continental basins and epicontinental seas occupied reduced areas leaving niches where wetland communities could arise (Fig. 4A). Water ferns first appeared in southern South America during this period of time (Kotova, 1983; Scafati and Morbelli, 1984).

Early Cretaceous: During the Early Cretaceous (Fig. 4B) seawater progressed onto the continent at both north (Venezuela and Colombia) and south (eastern Patagonia). This was due, in part, to the breakup of Gondwana and to the movements of the South American and African plates that produced Atlantic transgressions with the consequent flooding by shallow seas on the South American continent (Benedetto, 2010; Moulin et al., 2010; Maystrenko et al., 2013) and the Antarctic Peninsula. Only a few records were documented from southern South America before the Barremian (Archangelsky and Seiler, 1980; Cornú, 1986). Later on, towards the beginning of the Aptian, the endorheic internal basins expanded and the wetlands occupied larger areas, some of them connecting to oceanic waters (Fig. 4C), while uplands remained restricted and of moderate height (Graham, 2011). These processes occurred concomitantly with greenhouse effects conditions, equable climates, high and uniform mean annual precipitation, and low thermal and biodiversity gradients (Föllmi, 2012; Hu et al., 2012; Graham, 2011). As a result of these dynamic physical and climatic conditions many taxa were widely distributed and numerous new habitats developed that probably contributed to the rapid evolution and establishment of aquatic ferns.

Late Cretaceous: At the beginning of the Cenomanian South America and Africa were completely separated (Nürnberg and Müller, 1991). It is during the Cenomanian–Santonian (Fig. 4D) that a major subsidence of the south Atlantic margin began, causing a massive transgression and giving origin to the most extensive shallow epicontinental seas that characterized Patagonia at the end of the Cretaceous (Franzese et al., 2003; Malumián and Náñez, 2011). During this period, the maximum area of flooded inland areas and coastlines of South America was reached (Fig. 5A). Most probably, new habitats with abundant water supply, including those characterized by fresh water (such as lagoons and lakes) and brackish conditions (such as marshes, estuaries, and lagoon/barrier complexes), provided ideal niches for aquatic plants to thrive. In these environments, the water ferns had an obvious survival advantage because of their strategic adaptations to aquatic or semi-aquatic and/or changing habitats (such as the production of spores within sporocarps that ensures the viability of the contents over long periods of time, adaptation to drought, and high rate of vegetative reproduction by fragmentation) (Johnson, 1986; O'Connor et al., 2019) contributing to the group highest diversity ever recorded.

Cretaceous/Paleogene boundary: The environmental effects of the asteroid impact at the Chicxulub site (Chiarenza et al., 2020; Hull et al., 2020) indicate the boundary between the Cretaceous and the Paleogene in which the last mass extinction is recognized in Earth history. South American/Antarctic Peninsula Salviniales were affected (reduction in diversity and extinctions) by this global event as ~74% of the species and ~62% of the genera became extinct (Figs. 6 and 7).

Cenozoic: During the Cenozoic marine transgressions and epicontinental seas were widely distributed although maintained an overall steady decline (Guler et al., 2019, 2021). The few fossil genera that survived and crossed the boundary are restricted to the early Paleocene (i.e., *Ariadnaesporites*, *Azollopsis* and *Crybelosporites*) and only *Gabonisporis* is recorded until the mid-Eocene (Fig. 5B, Fig. 6). From then on, only the modern genera were recorded. The Antarctic Peninsula was devoid of aquatic ferns from the Paleocene onwards. During the late Eocene–early Oligocene (Fig. 5B), the complete separation of Antarctica from southern Patagonia and Australia led to the subsequent development of the Antarctic Circumpolar Current and the consequent thermal isolation of the Antarctic continent (Lawver and Gahagan, 2003; Brown et al., 2006). These geologic events added to the final uplift of the Andean Cordillera during the Neogene (Fig. 5C) (Ramos, 1999; Hartley, 2003), led to the modern climate of South America (Fig. 5D).

Most certainly all these tectonic movements and their associated changes in the topography and the climate contributed enormously to the evolutionary history and distribution of the Salviniales. Evolutionary responses to ecological opportunities are important in colonization of new disturbed habitats (Hoffmann and Hercus, 2000; Hoffmann and Sgrò, 2011) and, in the case of the Salviniales it helps to explain their diversification patterns in the fossil record (Collinson, 1991; Collinson et al., 2013). The crucial importance of the temporal correspondence between habitat opportunities and linage availability in shaping the evolution of the ecosystems was stressed by Graham (2012). Although aquatic and other freshwater or brackish habitats were present on Earth long before the Cretaceous, the concurrence in time and space of

physical environmental factors (mainly climate changes and geological events) and the accessibility of lineages that could underwent evolutionary changes to exploit new opportunities would explain the diversification of the group during the Cretaceous. The same forcing mechanisms (Graham, 2011) could have promoted the post Paleocene water ferns decline as the new habitats were exploited by other evolving and more successful groups probably represented by several lineages within the flowering plants.

4.3. Northern Hemisphere fossil record

Currently, there is not a comprehensive compilation of the fossil record of Salviniales for the Northern Hemisphere and therefore only partial comparisons with the data presented here can be made. The Northern Hemisphere Salvinialean fossil record is mostly based on dispersed spores (Batten and Kovach, 1990; Collinson, 1991, 2001; Batten and Collinson, 2001; Batten et al., 2011a, 2011b; Nandi and Chattopadhyay, 2003; Zavialova and Batten, 2018), although its macrofossil record has been increasing over the last decades (Collinson, 2001; Yamada and Kato, 2002; Aulenback, 2009; Sun et al., 2014; Wang et al., 2014; Pérez-Consuegra et al., 2017; Hermsen, 2019; among others).

Most water ferns fossil spore genera have a relatively widespread distribution in North and South America, Europe, Asia, Africa, and Australia, and they are mainly restricted to the Cretaceous (i.e., *Arcellites*, *Ariadnaesporites*, *Azollopsis*, *Balmeisporites*, *Crybelosporites*, *Gabonisporis*, *Ghoshispora*, *Molaspora*, and *Parazolla*). Only a few fossil spore genera appear to have an endemic distribution, which is restricted to the Late Cretaceous of some Northern Hemisphere regions [e.g., *Capulisporites* Potonié (Batten et al., 1994; Nandi and Chattopadhyay, 2003), *Glomerisporites* Potonié (Batten et al., 1998), and *Hallisporites* Nowak and Lupia (Nowak and Lupia, 2005)] or Southern Hemisphere regions (i.e., *Grapnelispora*, *Paleoazolla*, and *Thecaspora*).

Based mainly on the Northern Hemisphere record, several authors have proposed that the Salviniales diversified during the Late Cretaceous, with only the extant genera surviving into the Cenozoic (Rothwell and Stockey, 1994; Nandi and Chattopadhyay, 2003; Collinson et al., 2013). The few fossil genera that crossed the K–Pg boundary are almost entirely restricted to the early Paleocene. Similar results were obtained in the present study for South America and the Antarctic Peninsula.

5. Conclusions

We compiled 324 fossil records of the Salviniales including macro- (16 records) and microfossils (308 records) from South America and the Antarctic Peninsula. Marsileaceae is first recorded in the Middle to Late Jurassic, while Salviniaceae in the Late Cretaceous. Incertae sedis genera are recorded from Early Cretaceous to early Paleocene deposits. Two spikes in abundance and diversity are recognized, one in the Early Cretaceous, related to an increase in species diversity of Marsileaceae, and a second one during the Late Cretaceous associated with an increase at generic level of the entire salvinialean clade. One pauperization event is identified during the early Late Cretaceous which apparently only affected the species diversity of Marsileaceae. The major extinction event encompassed all Salviniales at generic and species levels and occurred between the Maastrichtian and the Danian (K–Pg extinction event). From the Paleocene onwards, most of the records are related to the extant genera.

Definitely, the Salviniales fossil record suggests that evolutionary responses (genetic and plastic changes) to ecological opportunities promoted by environmental changes, such as the paleogeographic configuration, the fluctuating sea levels with the development of wide epicontinental seas and the generalized distribution of wetlands environments, the global warm climate during the Cretaceous–Paleogene, the Cenozoic cooling, among other factors, played an important role in their past history.

Based on the evidence provided here, it is clear that aquatic ferns underwent a marked radiation during the Cretaceous and a deep decline from the Paleocene onwards in South America and the Antarctic Peninsula that parallels those proposed for the Northern Hemisphere, suggesting that additional studies of this group should be done globally to really understand their past history and perhaps their future.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.revpalbo.2021.104521.

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