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Salviniales from the Late Cretaceous of the Golfo San Jorge Basin

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ABSTRACT

The freshwater ferns (Salviniales) are well represented in the Maastrichtian deposits of Cerro de los Fragmentos in the headwaters of the Río Chico, Golfo San Jorge Basin. The fossil material of Salviniaceae includes complete megaspore apparatuses with attached microspore massulae and dispersed megaspores, float systems and microspore massulae of *Azolla*. The new species *Azolla colhuehuapensis* displays distinctive morphological characters including relative small megaspore apparatuses with easily detached floats and usually attached eglochidiate massulae. The Marsileaceae are represented by the megaspore *Molaspora lobata*, microspores of *Crybelosporites* and vegetative remains of *Marsileaceaephyllum* sp. The assemblage also includes zygospores of the green filamentous algae Zygnemataceae, spores of Marchantiophyta and Monilophyta (Schizaeales), megaspores of Isoetalean affinity and Palm-type angiosperm pollen grains. All these organic microfossils and the associated palynomorphs indicate the presence of a freshwater environment where abundant water ferns were developing and reproducing.

1. Introduction

The water ferns are a monophyletic group within the Order Salviniales Britton (Smith et al., 2006) and include the extant families Salviniaceae Martinov and Marsileaceae Mirbel (Smith et al., 2006; Christenhusz et al., 2011). They represent an important step in the evolution of modern heterospory, including for the first time since the origin of this reproductive strategy in the Palaeozoic, a single megaspore per megasporangium (a seed-like structure) (Nagalingum et al., 2006). They also present the most complex reproductive structures of the heterosporous plants, represented by the megaspores of the Salviniaceae (Hall, 1974; Batten and Collinson, 2001). They evolved in the Late Jurassic and diversified in the Late Cretaceous, with an excellent fossil record consisting of megaspores, microspores and vegetative remains (Lupia et al., 2000; Yamada and Kato, 2002; Martín-Closas, 2003; Vajda and McLoughlin, 2005; Nagalingum et al., 2006; Batten et al., 2011; Collinson et al., 2013). The water ferns are significant palaeoenvironmental indicators of fresh open-waters (photic zone) or wetlands (Collinson et al., 2013), with the extant Salviniaceae (*Azolla* and *Salvinia*) representing floating plants while the extant Marsileaceae (*Marsilea*, *Pilularia* and *Regnellidium*) include rhizomatous, semi-aquatic plants (Tryon and Tryon, 1982).

Salviniaceae from the Upper Cretaceous Patagonian deposits of Argentina include megaspore apparatuses and massulae of *Paleoazolla patagonica* Archangelsky et al., 1999 from the La Colonia Formation (Archangelsky et al., 1999; Cúneo et al., 2013, 2014) and dispersed massulae of *Azolla*, the latter including *A. cretacea* Stanley, 1965, *A.* (Rhizosperma) sp., *Azollopsis polyancyra* (Stough) Sweet and Hills, 1974, *A. circinata* Oltz and Hall, in Hall (1968) and *A.* spp. reported from the Loncoche, Allen and Paso del Sapo formations in Mendoza, Neuquén and Chubut provinces (Papú, 1988, 2002; Vallati, 2010; Puebla et al., 2014). Massulae of *Azollopsis polyancyra* have been also reported from the Upper Cretaceous deposits of the Austral Basin (Stough, 1968; Marenssi et al., 2004). The Marsileaceae megaspore *Molaspora lobata* (Dijkstra) Hall, in Hall and Peake (1968) and microspores of *Crybelosporites* have been reported from the La Colonia Formation (Cúneo et al., 2013; Cúneo et al., 2014; Hermsen et al., 2014).

The Upper Cretaceous megafossil record of Marsileaceae in Argentina includes leaves, leaflets, rhizomes and associated sporocarps from the La Colonia Formation of the Chubut province (Cúneo et al., 2013; Cúneo et al., 2014; Hermsen et al., 2014) and leaflets, rhizomes, roots, and a sporocarp-like structure from the Loncoche Formation of the Mendoza Province (Puebla et al., 2014).

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Salvinialean fossil remains consisting of massulae with septate glochidia, a single megaspore apparatus of *Azolla* and microspores of *Gabonisporis vigourouxii* Boltenhagen, 1967 have been reported from the uppermost part of the Lago Colhué Huapi Formation from a section outcropping at the headwaters of the Río Chico (Vallati et al., 2016). This palynoflora, included significant biostratigraphic markers of the upper Maastrichtian such as *Quadraplanus brossus* Stover and Partridge, 1973 and *Tubulifloridites lilliei* (Couper) Farabee and Canright, 1986.

In the present paper, we report additional aquatic plant material of the Salviniales from a nearby section at the headwaters of the Río Chico. The fossils include megaspore apparatuses, dispersed megaspores and massulae of the Salviniaceae as well as megaspores, microspores and vegetative remains of the Marsileaceae.

2. Geological setting

The Lago Colhué Huapi Formation was defined by Casal et al. (2015) for the lithostratigraphic interval in the uppermost part of the Chubut Group (Lesta and Ferello, 1972), which represents the main sedimentary filling in the Golfo San Jorge Basin (Fig. 1A–B). This unit overlies the Bajo Barreal Formation and underlies the Laguna Palacios Formation or the Salamanca Formation, according to its geographic position in the basin. The Lago Colhué Huapi Formation shows gradational top and basal contacts and occasionally an erosion surface (local unconformity) separates this unit from the Salamanca Formation (Casal et al., 2015; Vallati et al., 2016). In addition, at the studied locality (Fig. 1C), a laterally discontinuous basalt flow with a radiometric age of 67.31 ± 0.55 Ma (La Angostura Basalt) lies on top of the Lago Colhué Huapi Formation (Clyde et al., 2014).

The Cretaceous clastic and volcanoclastic deposits of the Chubut Group were interpreted as fluvio-lacustrine and fluvial systems. At its type locality, the Lago Colhué Huapi Formation, represents fluvial conditions of deposition with high-sinuosity channel systems and wide well-drained floodplains (Allard and Casal, 2013; Casal et al., 2015). This unit includes remains of titanosaurids, hadrosaurids and rare theropods (Casal et al., 2016), as well as plant remains (palynoflora, mesofossils and leaves) at the uppermost beds (Vallati et al., 2016; this paper).

The studied section, informally named Cerro de los Fragmentos, is a reduced outcrop (15 m thick), with an upward decreasing grain-size trend. It mainly includes medium to fine-grained sandstones that are interbedded with the reddish mudstones that characterize the Lago Colhué Huapi Formation (Fig. 2A–D). The high-sinuosity channel deposits recognized at Cerro de los Fragmentos are laterally related to proximal floodplain facies. The latter are represented by sandy to sandy-mud bodies of tabular geometry (sheet-like deposits) or flat-convex geometry (lobular deposits), as well as thin lentiform beds related to fluvial overflow. Furthermore, the red mudstones represent the deposits of distal floodplains, with the occasional presence of lagoon bodies (Casal et al., 2015).

This studied locality includes two fertile levels in the upper part of the Lago Colhué Huapi Formation. The lower layer (CF1 in Fig. 2A, D) contains the megaspores and the palynoflora presented herein. It is formed by grey fine to very fine-grained sandstones and limolites, up to 1 m thick, and with a lateral extension of tens of metres. This lithofacies is interpreted as a sheet-like non-channelized deposit. The upper layer containing the megafossil remains here reported, with the leaves of *Marsileaceaephyllum* (CF2 in Fig. 2A, C), is less than 10 cm thick, and overlies an erosion surface. The yellowish medium-grained sandstones, which are badly sorted, include plant remains with a disordered arrangement. This upper layer is a sheet-like deposit interpreted herein as the result of a high-density flow.

3. Materials and methods

3.1. Sample processing and study

The megaspores, palynomorphs and plant remains of the Salviniales were obtained from the beds CF1 and CF2 at Cerro de los Fragmentos in the headwaters of the Río Chico (Fig. 2A–D).

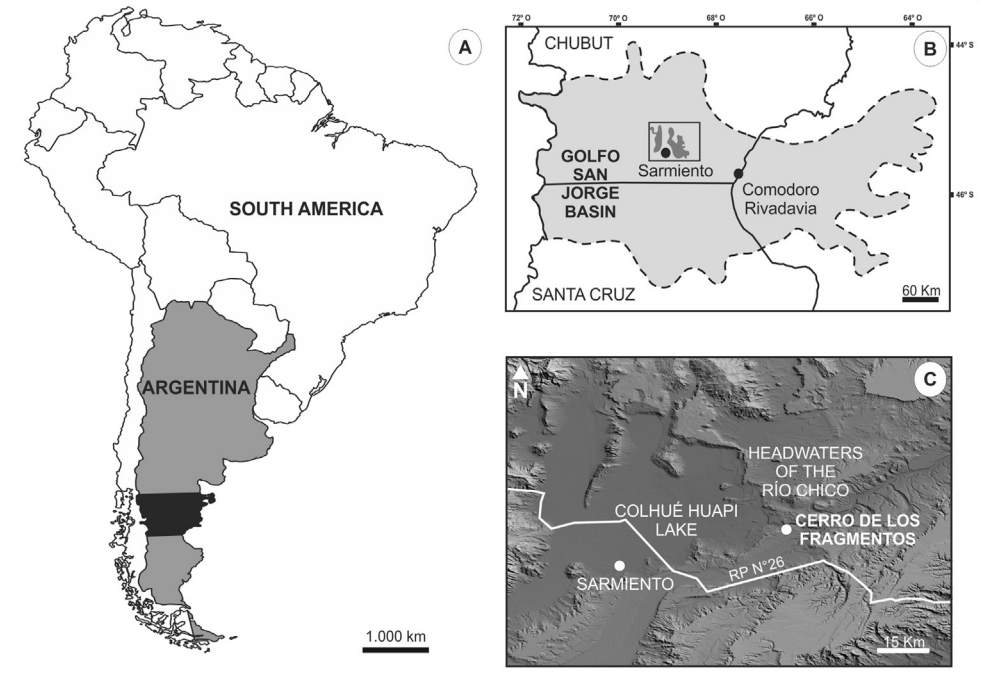

Fig. 1. Location map showing the studied locality Cerro de los Fragmentos in the headwaters of the Río Chico, Golfo San Jorge Basin.

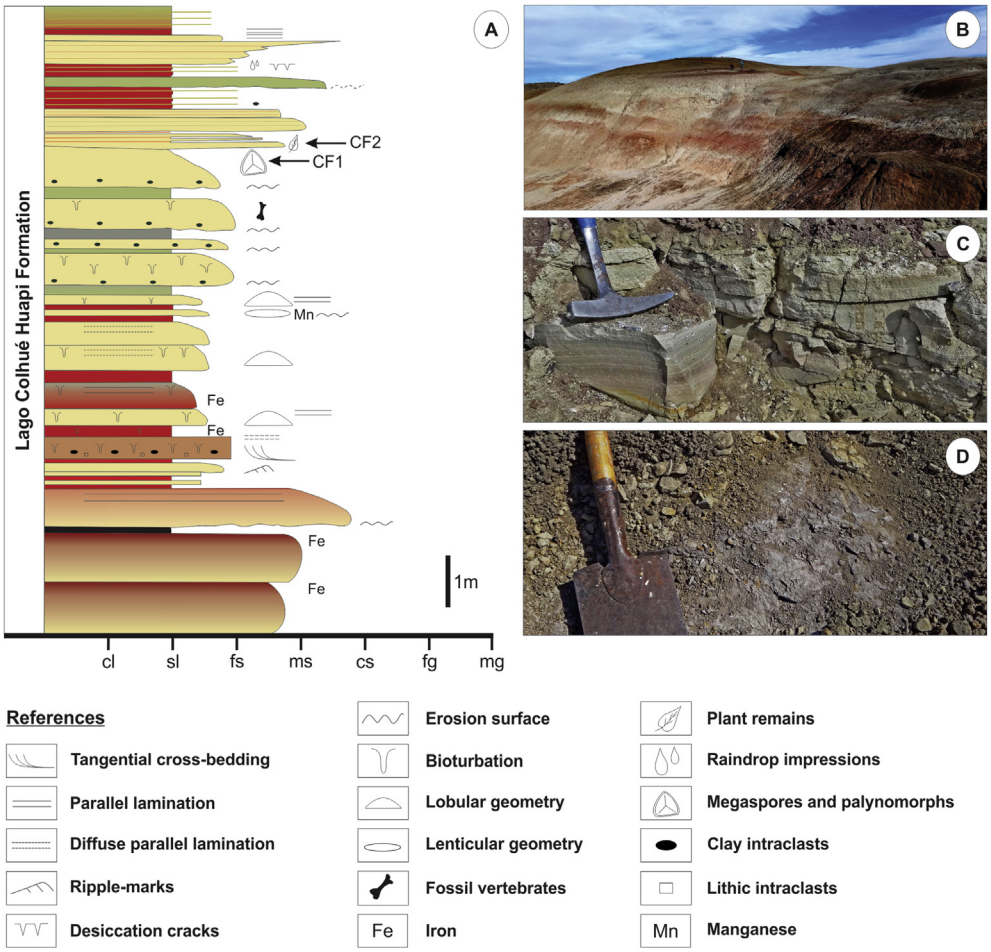

Fig. 2. A: Schematic section of the Lago Colhué Huapi Formation exposed at Cerro de los Fragmentos, with indication of the fertile levels CF1 and CF2. Lithological references. cl: clay; sl: silt; fs: fine sandstone; ms: medium sandstone; cs: coarse sandstone; fg: fine gravel; mg: medium gravel. The colours in the stratigraphic section do not represent the field colours of the rocks. B: Panoramic view of the studied section at Cerro de los Fragmentos. C: Fertile level CF2. D: Fertile level CF1.

The samples were mechanically disaggregated and treated with HF (70%) and HCl (19%).

The non-oxidized residue was wet sieved using mesh sizes 1.2 mm and 74 μm. Later, after being perfectly dried, it was sieved again and the megaspores were picked out under a stereo microscope (Motic SMZ-168) from fractions between 250 and 177 μm. Selected material was gold-coated (Quorum, Q150R ES) and photographed using a JEOL JSM-6510LV Scanning Electron Microscope at the Universidad Nacional de la Patagonia San Juan Bosco (UNPSJB). The mesofossils are housed in the micropalaeontological collection of the Scientific and Didactic Repository "Dr. Eduardo A. Musacchio" UNPSJB at Comodoro Rivadavia (catalogue numbers: UNPSJB-MFP 1-70).

Part of the residue was oxidated briefly using HNO3 (1–2 min) for light microscope (LM) examination. The samples were studied under a Carl Zeiss KF 2 microscope and the micrographs were taken with a digital Nikon Coolpix P2 camera at the Biostratigraphic Laboratory of the UNPSJB. The palynological slides are housed in the micropalaeontological repository at the UNPSJB, under the initials UNPSJB-MFP-CV. The palynomorphs are cited according to the corresponding slide identification followed by the coordinates of the Vernier Scale in the Zeiss Microscope.

The megafossils (compressions and impressions of leaves and leaflets) were collected by G. Casal in 2015 from the Cerro de los Fragmentos outcrop at the headwaters of the Río Chico. The examined material is housed at the repository of the UNPSJB under the catalogue number UNPSJB-PB 198-199.

3.2. Descriptive terminology

The megaspore apparatus of the Salviniaceae includes a distal megaspore and a proximal float system or swimming apparatus. The complex megaspore wall structure presents an internal layer or exine and the external layer or perine. The perine is generally divided into the endoperine and the ornamented exoperine from which may extend the hairs of the filosum. Regarding the filosum (covering of hairs over the megaspore apparatuses), the term infrafilosum is used for the hairs that cover the megaspore and the term suprafilosum for the hairs that arise from the modified exoperine of the collar region (Fowler and Stennett-Wilson, 1978; Batten and Collinson, 2001).

The term "float" is commonly used among researchers despite the fact that these proximal structures sink to the bottom of the water body at maturity (Fowler, 1975; Batten and Collinson, 2001; Vajda and McLoughlin, 2005; Collinson et al., 2010).

4. Systematic palaeobotany

Order Salviniales Britton, 1901
Family Salviniaceae Martinov, 1820

Genus *Azolla* Lamarck, 1783 (extant)
Type species: *Azolla filiculoides* Lamarck, 1783 (extant)

Azolla colhuehuapensis Vallati et al. sp. nov.
Figs. 3A–M, 4A–I

Holotype. Fig. 3A; UNPSJB-MFP 4
Paratypes. Fig. 3B, J–M (SEM), UNPSJB-MFP 37, 39, 40, 53, 56; Fig. 4A (LM), UNPSJB-MFP-CV 1a 3.5/100.
Repository. "Dr. Eduardo A. Musacchio" of the UNPSJB at Comodoro Rivadavia.
Type locality. Cerro de los Fragmentos at the headwaters of the Río Chico (45°38′2.86″S, 68°27′3.16″W).
Stratigraphic horizon. Maastrichtian, based on a palynoflora studied in a nearby exposure at the same locality (Vallati et al., 2016).
Derivation of name. From the stratigraphic unit Lago Colhué Huapi Formation in the Golfo San Jorge Basin that provided the megaspores and plant remains of the Salviniales.
Specific diagnosis. Megaspore apparatus pear-shaped, broader distally and covered by a mat of intertwined hairs or filosum. Megaspore spherical when uncompressed, with a smooth or faintly foveolate exine. Trilete mark with the laesurae extending about half of the radius of the spore. The proximal two-fifths of the megaspore apparatus occupied by the float system. Nine easily detachable floats arranged in two tiers, with three larger floats in the upper tier and six smaller floats in the lower tier. Floats loosely enmeshed by hairs of the filosum in compartments of prismatic geometry separated by a dense hairy wall. Floats with spongy vacuolated appearance under LM.

Microspore massulae usually one cluster per megaspore, eglochidiate, alveolate with the regular alveoli showing distinctive subcircular to sub-polygonal boundaries. Over 30 trilete microspores with the laesurae extending the whole radius.

Material. More than a hundred complete megaspore apparatuses, several detached megaspores, float systems and massulae were collected from the uppermost levels of the Lago Colhué Huapi Formation at Cerro de los Fragmentos in the Golfo San Jorge Basin. Most of the material proceeds from CF1 with few specimens collected from CF2 (Fig. 2A–D). Five complete megaspore apparatuses, 10 dispersed massulae, 10 dispersed floating systems or part

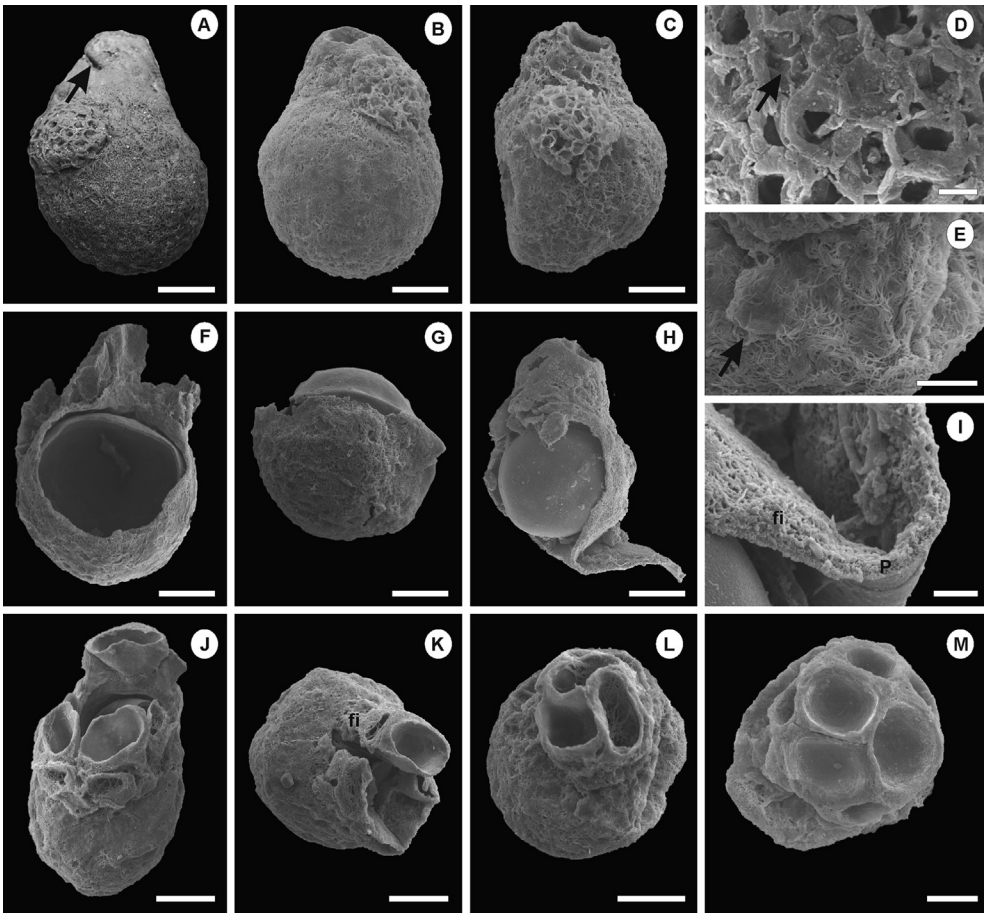

Fig. 3. *Azolla colhuehuapensis* sp. nov. from the Lago Colhué Huapi Formation at Cerro de los Fragmentos, Golfo San Jorge Basin. SEM micrographs (A–C, F–H, J–L), scale bars: 50 μm; (D, E, J), scale bars: 10 μm. A. Holotype. Megaspore apparatus in lateral view, with covering of filosum and an attached microspore massula at the proximal end of the megaspore. Microspores are present in some of the massula alveoles. One preserved float is visible (arrow), UNPSJB-MFP 4. B. Paratype. Megaspore apparatus in lateral view, with covering of filosum and an attached microspore massula, UNPSJB-MFP 39. C. Megaspore apparatus with the filosum. The alveolate nature of the massula is clearly visible, UNPSJB-MFP 46. D. Detail of the massula, with some microspores with the trilete marks visible (arrow), UNPSJB-MFP 66. E. Detail of the megaspore wall of specimen L. A microspore enmeshed in the hairs of the infrafilosum is indicated by an arrow, UNPSJB-MFP 37. F. Naturally broken specimen showing the smooth exine and the perine of the megaspore, UNPSJB-MFP 54. G. Megaspore with covering of infrafilosum, revealing the smooth exine, UNPSJB-MFP 57. H. Naturally broken specimen, showing the smooth exine and the alveolate perine of the megaspore and the float system, UNPSJB-MFP 65. I. Detail of the perine (**P**) and filosum (**fi**) in specimen H. Note the faintly foveolate exine of the megaspore, UNPSJB-MFP 65. J. Paratype. The float system with the compartments of prismatic geometry without floats preserved. Three larger compartments of the upper tier and three out of six smaller of the lower tier. Long hairs can be seen inside the compartments, UNPSJB-MFP 56. K. Paratype. Megaspore apparatus in oblique view. Note the filosum (**fi**) and the faintly foveolate inner surface of the float compartments, UNPSJB-MFP 53. L. Paratype. Megaspore apparatus in apical view, showing the apertures of the upper compartments and hairs of the suprafilosum, UNPSJB-MFP 37. M. Paratype. A specimen in apical view, showing the three upper compartments, four lower and the layer of tomentose texture separating them, UNPSJB-MFP 40.

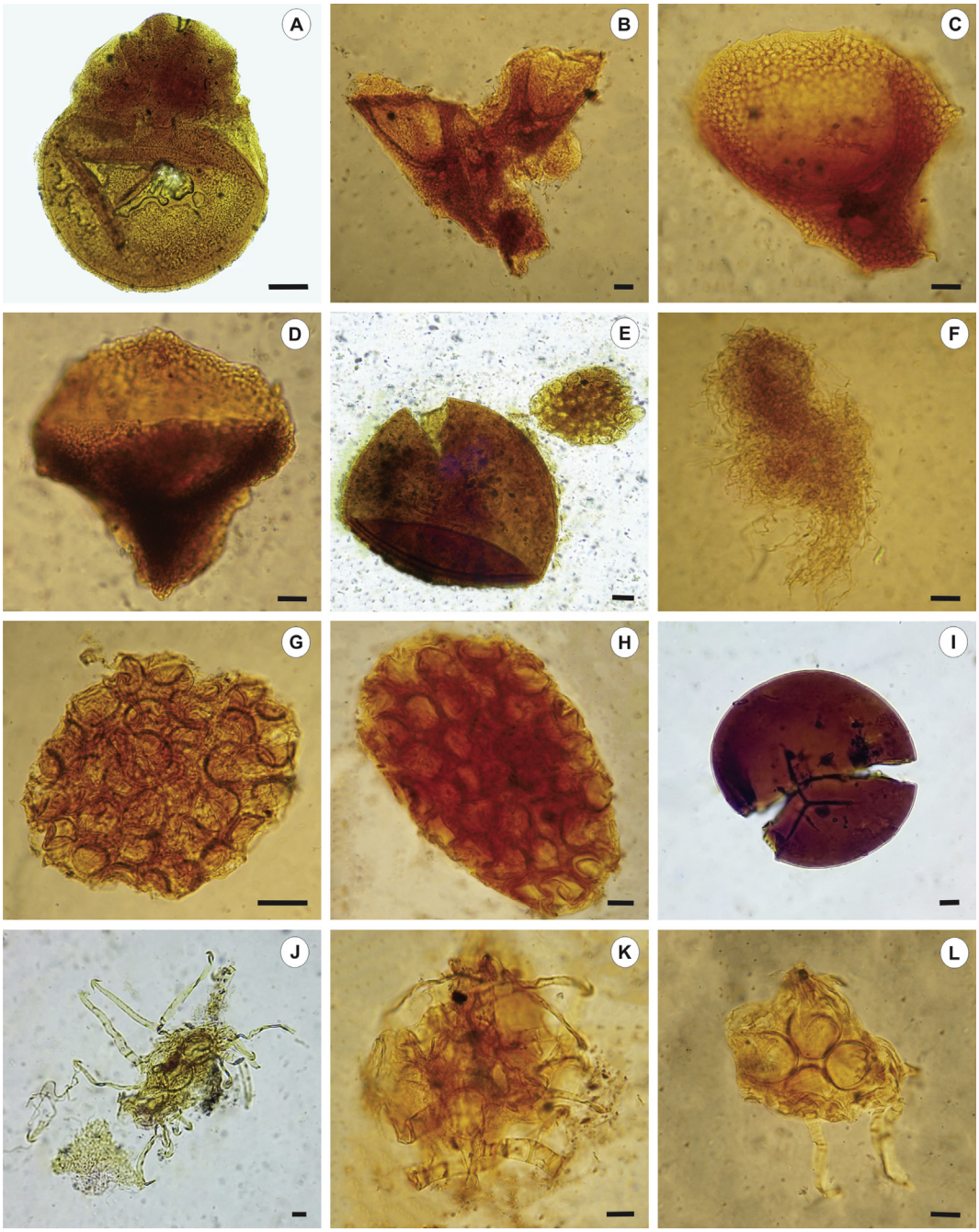

Fig. 4. *Azolla colhuehuapensis* sp. nov. (A–I) and *Azolla* sp. 2 (J–L) from the Lago Colhué Huapi Formation in the Golfo San Jorge Basin. LM micrographs (A), scale bar: 50 μm; (B–L), scale bars: 10 μm. A. Megaspore apparatus, showing the distal megaspore and the float zone, UNPSJB-MFP-CV 1a 3.5/100. B. Part of the float system showing floats and the layer of tomentose texture separating them, UNPSJB-MFP-CV 1L 22/104. C. Dispersed cavity with float, UNPSJB-MFP-CV 1L 11/81. D. Dispersed cavity with float, UNPSJB-MFP-CV 1V 16/89. E. A megaspore covered by the filosum and a microspore massula partially attached, UNPSJB-MFP-CV 1b 18/97. F. Fragment of filosum, UNPSJB-MFP-CV 1b 6/96. G. Massula with some trilete microspores preserved, UNPSJB-MFP-CV 1Z1 15/105. H. Massula with some trilete microspores preserved, UNPSJB-MFP-CV 1U 16/94. I. Trilete megaspore, showing the smooth exine and the trilete mark, UNPSJB-MFP-CV 1 Z1 5/103. J. Massula showing fully developed septate glochidia and anchor-shaped tips. Note the anchor-shaped tips entwined in hairs of the filosum (arrow), UNPSJB-MFP-CV 1J 10/100. K. Massula with many glochidia folded inward, UNPSJB-MFP-CV 1L 19/98. L. Massula showing four circular microspores and septate folded and radiating glochidia, UNPSJB-MFP-CV 2 15/95.

of them were studied by LM. Twenty complete megaspore apparatuses and ten isolated megaspores were studied by SEM.

Description. The megaspore apparatus is typically pear shaped and broader distally (190–358.5 μm long and up to 286 μm wide, more than twenty specimens measured), always longer than broad (Fig. 3A–C, H; Fig. 4A). The entire megaspore apparatus is covered by a relatively thick mat of intertwined hairs (filosum), which are 0.5–1.7 μm wide and present a smooth surface (Fig. 3A–C, F–L; Fig. 4A).

Megaspore. Several dispersed megaspores were found in the palynological slides (Fig. 4E, I). The megaspores are spherical when uncompressed, and they present a wall that includes a smooth to faintly foveolate exine (up to 5.4 μm thick) and a perine (up to 6.7 μm thick). The perine is alveolate and covered by the hairs of the

filosum (Fig. 3F, H, I). The laesurae of the trilete marks have a mean length of 45 μm (five specimens measured) and extend to about half of the radius of the megaspore (Fig. 4E, I).
Float system. The float system occupies at least the proximal two-fifth of the megaspore apparatus (Fig. 3A–C, H). There is no evidence of a collar in the basal zone of the float system. A layer of tomentose texture (densely interwoven hairs) delimits the compartments that house the floats as shown in Figs. 3J, 4B. This structure derived from intertwined hair-like filaments can be considered a columella (Batten and Collinson, 2001). The floats show a vacuolated structure (Fig. 4C, D). Two tiers of floats are present, with three larger upper and six smaller lower floats. The floats are enmeshed by hairs of the filosum (Fig. 3J, L). Under LM internal nucleus can be seen inside the float system (dark spots in Fig. 4B), probably representing the centre around which the foamy structure of the float was organized (Hall and Bergard, 1971). The floats are loosely entangled by hairs of the columella and consequently easily detached from the float system, giving rise to a great number of specimens devoid of floats. The float system presents frequently empty prismatic (sub-conic) cavities with smooth or faintly foveolate inner surfaces (Fig. 3J–M).
Massulae. The massulae are eglochidiate, and their surfaces lack hairs (Figs. 3B, D, 4E, G, H). They are up to 122 μm in diameter and they are usually found attached to the proximal end of the megaspore. One massula per megaspore is normally present or, in a few specimens, up to two. Many dispersed massulae were also recognized in the palynological slides (Fig. 4G, H). The massulae have many funnel shaped alveoli with circular to subpolygonal boundaries containing each a smooth-walled trilete microspore (Fig. 3D). The microspores are around 12 μm in diameter and the laesurae of the trilete mark are 5.8–7.0 μm long extending the whole radius of the spore (Fig. 3D).
Remarks. *A. colhuehuapensis* sp. nov. is placed in the subgenus *Azolla* section Rhizosperma which includes species that have megaspore apparatuses with nine floats always distributed in the same way: three larger upper and six smaller lower floats, and glochidia absent or reduced to simple structures inside the massulae (Saunders and Fowler, 1992). Nine-floated species with eglochidiate massulae include the extant species *Azolla nilotica* Decne. ex Mett in Kotschy and Peyritsch, 1867 and *Azolla pinnata* Brown, 1810 (the latter including glochidia represented by simple hairs). Among other differences, both living species differ from *A. colhuehuapensis* in the absence of entanglement threads covering the megaspore (Lumpkin, 1981). The Cenozoic species *A. nana* Dorofeev, 1959, *A. turgaica* Dorofeev, 1959 and *A. ventricosa* Nikitin, 1965 with nine floats, differ from the new species in several morphological characters.

A similar *Azolla*-like specimen without floats was illustrated by Cúneo et al. (2014) from the Cretaceous La Colonia Formation in the Chubut Province. No description was included by the authors impeding further comparisons.

Even though Hall and Bergard (1971) stated that the number of massulae attached to the megaspore does not represent a useful character for specific distinction, because it seems to be conditioned by the preservation and the number of massulae produced, this is a consistent character in this species.

Azolla sp. 1
Fig. 5A–D, F

Material. Five complete megaspore apparatuses studied by SEM and several detached megaspores in samples UNPSJB-MFP 20, 41, 43, 48, 69 from the uppermost levels of the Lago Colhué Huapi Formation at Cerro de los Fragmentos, Golfo San Jorge Basin (CF1, Fig. 2A, D).

Description. Oval megaspore apparatus (242–259 μm long) clearly differentiated into the megaspore and the float system. The collar (up to 17.6 μm thick) originates from the perine in the apical part of the megaspore (Fig. 5D). The megaspore wall includes an alveolate perine with the surface covered by granules, verrucae of different sizes and tuberculate or columnar perine excrescences (Fig. 5A–D), which can partially or completely coalesce forming rugulae. Similar tuberculate and rugulate excrescences are present on the megaspore wall of some specimens of the Eocene species *Azolla jutlandica* (Collinson et al., 2010). Scattered short hair-like filaments are visible near the tubercles on the surface of the megaspore (Fig. 5D), while hairs of the filosum (suprafilosum) are associated to the floats (Fig. 5B–C). The dome shaped float system occupies one half of the megaspore apparatus. Three compartments with the attached floats are delimited by an extension of the proximal wall of the megaspore (Fig. 5A). A tomentose layer, with densely intertwined hairs of the filosum forms the tripartite columellar structure (Fowler, 1975; Batten and Collinson, 2001) (Fig. 5A, B). Each of the compartments houses the vacuolated floats. Three vacuolated floats (or three float partitions) are visible in the specimen of Fig. 5B, but the total number of floats is not yet clearly defined. The alveoli of the floats (Fig. 5A) have a diameter that diminishes from the centre (16 μm) to the periphery (6.5 μm).
Remarks. No massula was found attached on the megaspore surface and the number of proximal floats is uncertain, hence the identification of this type is left in open nomenclature.

A megaspore apparatus of *Azolla* sp. 1 was illustrated in Fig. 4, 15 by Vallati et al. (2016) from another section at the same locality.

A similar arrangement of floats between partitions of a tripartite columella is present in the Oligocene species *Azolla prisca* (Reid & Chandler) Fowler, 1975 with nine floats and in the Eocene *Azolla jutlandica* Collinson et al., 2010, with six or nine floats distributed in one tier (Collinson et al., 2010).

Azolla sp. 2
Fig. 4J–L

Material. Several massulae studied in palynological slides from levels CF1 and CF2 (Fig. 2) from the uppermost level of the Lago Colhué Huapi Formation at Cerro de los Fragmentos in the Golfo San Jorge Basin.
Description. The massulae have an oval outline, and include a reduced number of trilete microspores (normally 4) with a circular outline, that are enmeshed in a pseudo-vacuolated tissue. The surface of the massula is faintly granulated (Fig. 4J–L). The glochidia are relatively large (up to 75 μm), but some shorter glochidia are also present (Fig. 4J). They are variously septate with anchor-shaped tips that narrow distally. The hooks are typically not recurved, but anchor tips with recurved hooks are also appreciated in some specimens. The variable nature of this character was already observed for another species of *Azolla* (Van der Burgh et al., 2013). The stalks have a distal dilation and a constriction beneath the anchor-shaped tips (Fig. 4J). Occasionally, a bifurcation of the septa occurs near the contact with the stalk walls (Fig. 4K).
Remarks. The massulae illustrated in Vallati et al. (2016, Fig. 4.13) probably belongs to the species *A.* sp. 2 from Cerro de los Fragmentos, as they share distinctive morphological characters including the granulate surface of the massula, the number of microspores and the septate glochidia with anchor-like tips.

Family Marsileaceae Mirbel in Lamarck and Mirbel, 1802

Genus *Molaspora* (Schemel) Hall, 1963
Type species: *Molaspora lobata* (Dijkstra) emend. Hall in Hall and Peake, 1968

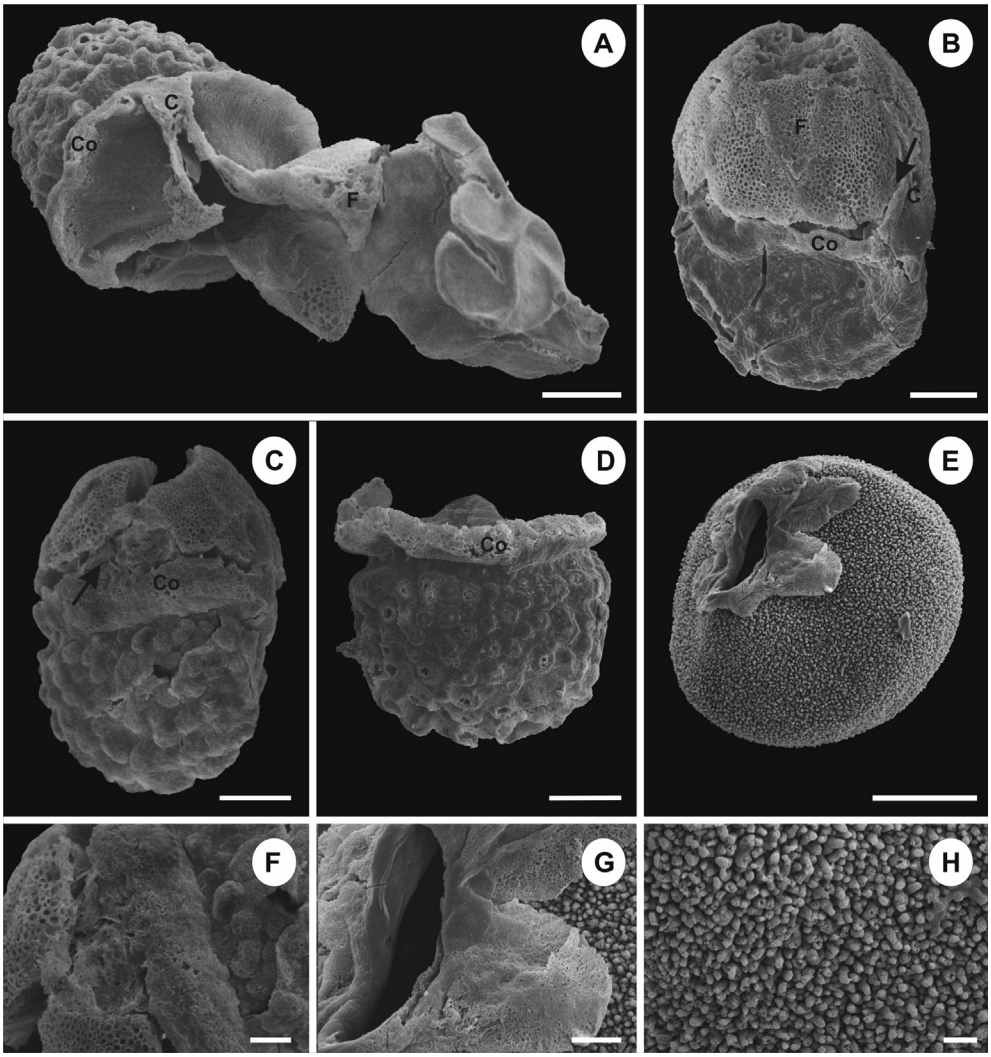

Fig. 5. Mesofossils of Salviniaceae (*Azolla* sp.1; A–D, F) and Marsileaceae (*Molaspora lobate*; E, G–H) from the Lago Colhué Huapi Formation, Golfo San Jorge Basin. SEM micrographs (A–E), scale bars: 50 μm; (F–H), scale bars: 20 μm. A. Damaged megaspore apparatus shows the megaspore with some coalescing perine excrescences and the collar (**Co**) separating it from the float system. The tripartite columella (**C**), the three compartments and disaggregated floats (**F**) are visible, UNPSJB-MFP 41. B. Complete megaspore apparatus with the vacuolated floats (**F**) and part of the columella (**C**) visible above the collar (**Co**), UNPSJB-MFP 43. The arrow is indicating the hairs associated to the floats. C. Complete megaspore apparatus with the collar (**Co**) and the float system visible, UNPSJB-MFP 48. The arrow is indicating the hairs associated to the floats. D. Dispersed megaspore, showing the collar (**Co**). Tuberculate perinal excrescences including short hair-like structures near the tubercles, UNPSJB-MFP 47. E. Megaspore with the triangular lobes of the acrolamella folded over the surface around the aperture, UNPSJB-MFP 52. F. Detail of image C showing the hairs of the suprafilosum arising from the collar, UNPSJB-MFP 48. G. Detail of image E showing the alveolate character of the lobes of the acrolamella and the smooth inner surface of the aperture, UNPSJB-MFP 52. H. Detail of image E showing the baculate perine of the megaspore wall, with some baculae with inflated apices, UNPSJB-MFP 52.

Molaspora lobata (Dijkstra) emend. Hall in Hall and Peake, 1968
Fig. 5E, G, H

Material. Two specimens were recovered from CF1 (Fig. 2A–C) of the Lago Colhué Huapi Formation at Cerro de los Fragmentos in the Golfo San Jorge Basin.
Description. Dispersed megaspore with an originally spheroidal shape (Fig. 5E), 311 μm wide and 200 μm the polar axis. The figured specimen shows the subtriangular lobes of the acrolamella on the proximal pole surrounding the aperture and folded over the surface of the megaspore (Fig. 5E, G). They are up to 88 μm long and up to 67 μm wide. The specimen UNPSJB-MFP 70 (not illustrated) shows the aperture closed and the typical twisted lobes. The sculpture of the spore body is baculated, with relatively regular baculae, some of which show inflated apices (Fig. 5H), as it was already observed in specimens of *Molaspora lobata* studied by Lupia (2011).

Crybelosporites Dettmann, 1963

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

Crybelosporites sp.
Fig. 6E

Material. Up to 6 specimens were recovered from the Lago Colhué Huapi Formation at Cerro de los Fragmentos, Golfo San Jorge Basin (CF1 and CF2 in Fig. 2A–D).
Description. The specimens are spheroidal with a smooth sclerine and a proximally cavate and sculptured perine. They are 40–43 μm in diameter. The perine (3–6.5 μm) is rugulo-reticulate and forms an irregular reticulum. The laesurae, when visible, extend to half of the radius of the inner body and they are near 6 μm long (Fig. 6E).

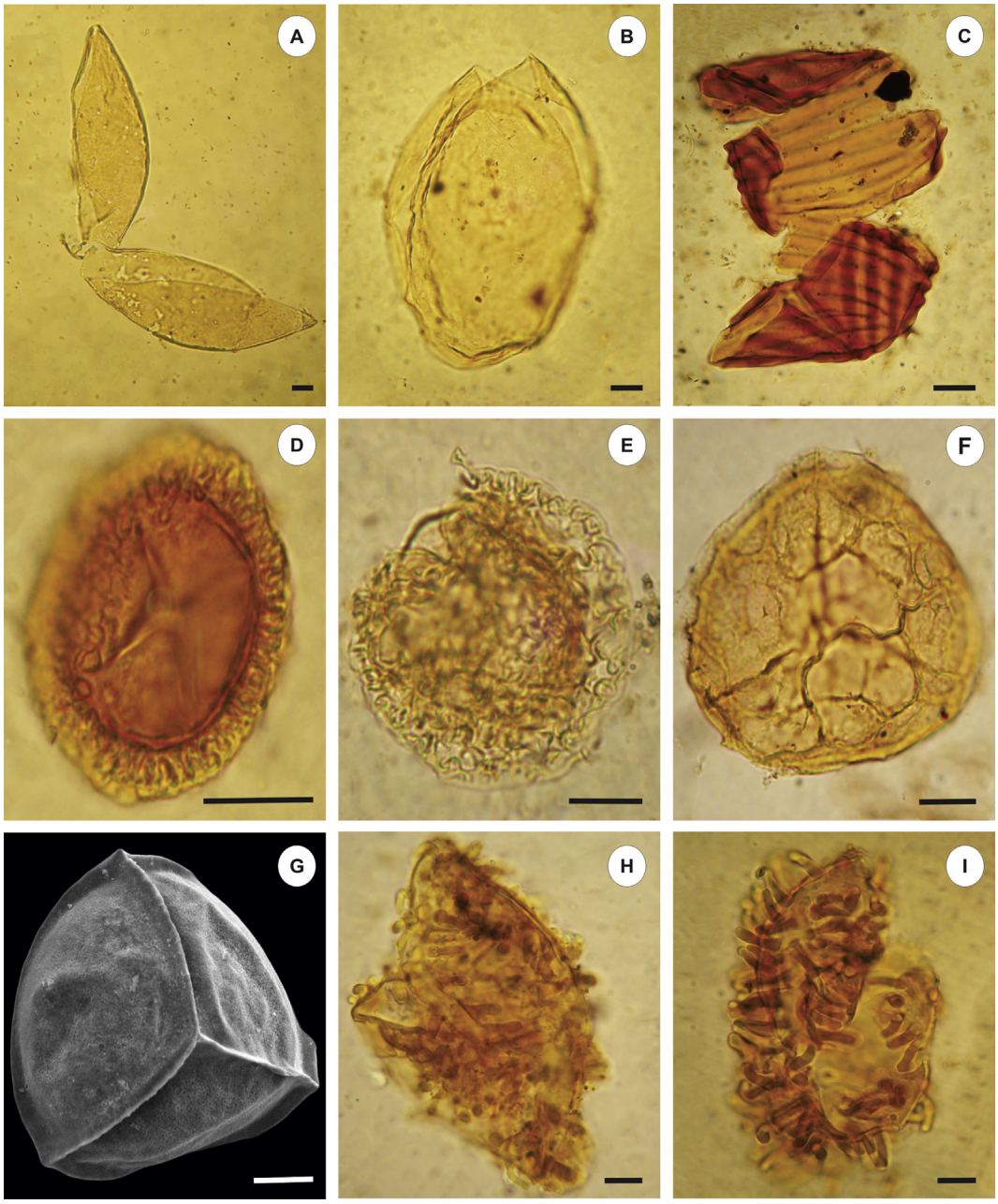

Fig. 6. Associated palynomorphs from the Lago Colhué Huapi Formation at Cerro de los Fragmentos, Golfo San Jorge Basin. LM micrographs (A–F, H–I), scale bars: 10 μm. SEM micrograph (G), scale bar: 50 μm. A. *Ovoidites* sp., UNPSJB-MFP-CV 1 16/113. B. *Ovoidites* sp., UNPSJB-MFP-CV 1f 14/95. C. *Cicatricosisporites* sp., UNPSJB-MFP-CV 1b 11/110. D. *Gabonisporis vigourouxii*, UNPSJB-MFP-CV 1L 16/100. E. *Crybelosporites* sp., UNPSJB-MFP-CV 1V 16/94. F. *Zlivisporis reticulatus*, UNPSJB-MFP-CV 1J 5/87.G. *Minerisporites* sp., UNPSJB-MFP 11. H. *Spinizonocolpites* cf. *hialinus*, UNPSJB-MFP-CV 1C 14/98. I. *Spinizonocolpites* cf. *hialinus*, UNPSJB-MFP-CV 1 10/101.

Plant megafossils
Family Marsileaceae Mirbel in Lamarck and Mirbel, 1802

Genus *Marsileaceaephyllum* (Nagalingum) emend Hermsen, Gandolfo and Cúneo, 2014
Type species: *Marsileaceaephyllum johnhallii* (Skog and Dilcher) Nagalingum, 2007

Marsileaceaephyllum sp.
Fig. 7A–E

Material. Leaves and leaflets from the Lago Colhué Huapi Formation at Cerro de los Fragmentos (CF2, in Fig. 2A–D).
Description. The remains from Cerro de los Fragmentos (CF2, in Fig. 2A–D) consist of very small compound leaves with four leaflets that are joined basally in a cruciform arrangement. The leaflets are obovated with rounded apexes, 2–2.5 mm long and 2 mm wide, and they have an entire margin. When visible, the venation is dichotomous with anastomoses that leave hexagonal and longitudinally extended areoles (Fig. 7E). A marginal vein or part of it is clearly visible (Fig. 7D). The petiole of the leaves is unknown and a midvein is absent. The cruciform arrangement of the four leaflets of *Marsileaceaephyllum* sp., matches extant *Marsilea* (Fig. 7F).
Remarks. *Marsileaceaephyllum* is a morphotaxon originally described by Nagalingum (2007) to encompass dispersed leaves of marsileaceous affinity mostly based on the vein pattern. Recently, Hermsen et al. (2014) emended the genus and restricted it to fossil leaves with four leaflets, a venation dichotomizing with few

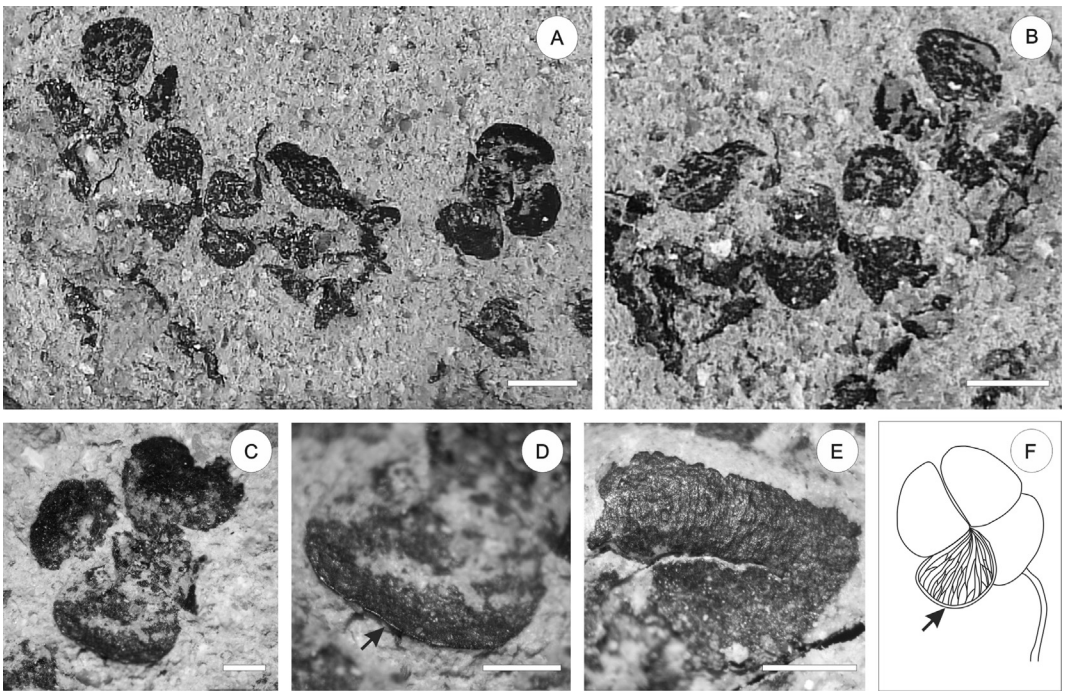

Fig. 7. *Marsileaceaephyllum* sp. from the Lago Colhué Huapi Formation at Cerro de los Fragmentos, Golfo San Jorge Basin. (A–B), scale bars: 3 mm; (C–E), scale bars: 1 mm. A–B. Leaves and leaflets of *Marsileaceaephyllum* sp., UNPSJB PB 198–199. C. Leaf with three leaflets preserved in a cruciform pattern, UNPSJB PB 198.D. Detail of a leaflet from image C showing the marginal vein (arrow), E. Detail of a leaflet from another specimen (not illustrated) showing the venation pattern, UNPSJB PB 199. F. Schematic diagram of a *Marsilea* leaf showing the marginal vein (arrow) and the venation pattern.

anastomoses to reticulate and a marginal vein present. Even though the preservation of the present material hinders a good recognition of the venation in some of the studied specimens, the presence of four obovate leaflets in a cruciform pattern, and a marginal vein clearly present justifies the inclusion of this material in the genus *Marsileaceaephyllum*.

5. Discussion

The Salviniaceae species *A. colhuehuapensis* displays easily detachable floats as one of its most distinctive characters. This feature is probably related to the presence of relative scarce hairs available to retain them (Hoffman and Stockey, 1994). Most of the megaspores of *A. colhuehuapensis* have the massulae attached, suggesting that the material was dispersed as part of the natural reproductive cycle (Barke et al., 2012).

The Salviniaceae are represented as well by the megaspore apparatuses of *Azolla* sp. 1, which lack a distinctive surface coat of filosum and the glochidiate massulae of *Azolla* sp. 2. These two latter species were not found in organic connection. Even more, the septate glochidia of *A.* sp. 2 were found entangled to fragments of large hairs (Fig. 4J), suggesting that these two reproductive structures could belong to different plants.

Few reports of megaspores of *Azolla* are known from the Cretaceous of South America. Vajda and McLoughlin (2005) reported *Azolla boliviensis* from the Maastrichtian deposits of the Eslabon Formation in Bolivia. The megaspore apparatus of this species bears nearly 30 subcircular floats with glochidiate massulae and aseptate anchor-shaped glochidia. Considering the record of Cretaceous Patagonian megaspore apparatuses, *Paleoazolla patagonica* recognized in the Maastrichtian La Colonia Formation of the Chubut Province has a float system with three to four floats and massulae with multibarbed glochidia. The dispersed megaspore *Molaspora lobata*, the microspores assigned to *Crybelosporites* and probably *Gabonisporis* (see Quattrocchio et al., 2000) found in the present assemblage of Cerro de los Fragmentos have affinity to the Marsileaceae. The joint presence of megaspores of *Molaspora lobata* and *Crybelosporites*-like microspores was already mentioned by Hall (1967). Moreover, marsileaceous sporocarps assigned to the extant genus *Regnellidium* Lindman, 1904 with *in situ Molaspora lobata* and *Crybelosporites*-like microspores were reported by Lupia et al. (2000) from the Upper Cretaceous of Georgia, United States. The marsileaceous assemblage of the La Colonia Formation includes these two taxa from the same layers where *Regnellidium* was collected (Cúneo et al., 2014). These records, as well as the morphological characters of the extant forms, suggest the relation of these reproductive structures to extinct *Regnellidium*-like plants (see Lupia et al., 2000 for discussion).

Marsileaceaephyllum, which is represented by leaves and leaflets from Cerro de los Fragmentos, has affinity to extant *Marsilea*. Hermsen et al. (2014) suggested that the megaspores of *Molaspora* could be associated with *Marsileaceaephyllum* during the Cretaceous. In this regard, it is interesting to consider that Cretaceous fossils could exhibit a different combination of features compared to that seen in living plants (Lupia et al., 2000). Hermsen et al. (2014) have reported leaves with a *Marsilea*-like venation from the La Colonia Formation. These fossils include two petiolulate leaflets and were assigned to the extinct genus *Mirasolita* Hermsen et al., 2014.

The palynological assemblages studied also include zygospores of Zygnemataceae as *Ovoidites* sp. and *Catinipollis geiseltalensis* Krutzch, 1966; spores of Marchantiophyta as *Zlivisporis reticulatus* (Pocock) Pacltová and Simoncsics, 1970, Lycophyta (Isoetaceae) as *Minerisporites* sp. and Monilophyta (Schizaeales) as *Cicatricosisporites* sp. (Fig. 6A–I). The angiosperm pollen grains are mainly represented by *Spinizonocolpites* cf. *hialinus* Archangelsky and Zamaloa, 1986 (Fig. 6H, I), which probably represents the pollen

of extant Arecaceae (Nypa-type). A similar palynological assemblage was recently reported from another section at the headwaters of the Río Chico (Vallati et al., 2016). The aquatic community of the lower bed studied at Cerro de los Fragmentos (CF1 in Fig. 2A, D) is dominated by the surface-floating heterosporous fern *Azolla*. The upper bed (CF2 in Fig. 2A, C), with a poorer assemblage of palynomorphs and megaspores, includes the leaves and leaflets assigned to *Marsileaceaephyllum* here described, as well as other plant remains that are now under study.

The rich assemblage of *Azolla* studied herein could be explained taking into account ecological factors that affect the growth of living *Azolla* (Speelman et al., 2009; Espinar et al., 2015). Therefore, the abundance of *Azolla* in the Upper Cretaceous of central Patagonia may have been influenced by local changes in water quality (eutrophication mainly due to high phosphorous concentrations) or favourable climatic conditions (increase in average temperature, atmospheric carbon dioxide enrichment) that would have allowed the plants to grow fast.

These Maastrichtian aquatic communities at the headwaters of the Río Chico will probably contribute to better understand the environmental conditions prevailing at this paleolatitude in a critical interval prior to the K/Pg event.

6. Conclusions

The Salviniales are well represented at Cerro de los Fragmentos in the headwaters of the Río Chico, Golfo San Jorge Basin. This record supports the widespread distribution of the heterosporous plants in the Maastrichtian of Patagonia.

The new species here described *A. colhuehuapensis* dominates the palynological and the mesofossil assemblages. The presence of different species of *Azolla* in the uppermost levels of the Lago Colhué Huapi Formation confirms the Cretaceous record of extant taxa.

The abundance and diversification of *Azolla* is probably suggesting a rapid event of colonization of the newly formed freshwater bodies in the floodplains by these invasive and faster growing plants.

The leaves and leaflets of *Marsileaceaephyllum* from Cerro de los Fragmentos represent the first record of this taxon with affinity to extant *Marsilea* in Argentina.

These Salviniales from the upper beds of the Lago Colhué Huapi Formation and the associated palynomorphs, represent the aquatic flora and the terrestrial local vegetation that grew in a freshwater body and around it.

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