

Aquatic ferns from the Upper Cretaceous Loncoche Formation, Mendoza, central-western, Argentina

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Abstract Herein, we report new fossil remains with marsileaceous affinity associated with dispersed microspores corresponding to *Crybelosporites*, different types of massulae of Salviniaceae (*Paleozolla patagonica* and *Azolla circinata*), and a single megaspore assigned to the fossil genus *Grapnelispora*. These fossils were recovered from the Late Cretaceous Loncoche Formation, at the Calmu-Co section, Malargüe Group, Northern Neuquén Basin, Mendoza, Argentina. The macrofossils include scattered leaflets, rhizomes, roots, and a sporocarp-like structure. They share characters with members of the aquatic fern family Marsileaceae; however, based on the characters preserved, they could not be placed within any extant or fossil species; therefore, the fossils are better included within a new fossil-taxon, *Mendozaphyllum loncochense*. Dispersed spores of *Crybelosporites pannuceus*, also belonging to Marsileaceae, were recovered from the entire section. Additionally, abundant isolated massulae with affinity to the aquatic fern family Salviniaceae, and a single megaspore assigned to *Grapnelispora loncochensis*, were identified from the plant bearing layer. The presence of Marsileaceae fossils in the Campanian–Maastrichtian Loncoche Formation, Mendoza, extends towards the north the paleogeographical distribution of the family Marsileaceae in Argentina, since previous records are from Patagonia. A

fluvial to deltaic environment with lacustrine episodes is suggested by the sedimentology of the lower and middle parts of the Calmu-Co section and supported by the abundant fresh water algae recovered from the palynological association. This was probably the optimum habitat for the growth of aquatic ferns related to Marsileaceae and Salviniaceae and explains its abundance in the studied sediments.

Keywords Heterosporous ferns · Fossil remains · Upper Cretaceous · Argentina

Introduction

Heterosporous ferns are a monophyletic group within the Order Salviniales Bartling and include two extant families: Marsileaceae Mirbel and Salviniaceae Martinov (Smith et al. 2006). Salviniaceae are floating aquatics, whereas Marsileaceae are rooted and semi-aquatic. Living Salviniaceae is represented by two genera, *Salvinia* Seg. (ca. 10 species) and *Azolla* Lam. (6 species). *Salvinia* occurs in South and North America, Africa, Madagascar, Europe, and Asia while *Azolla* is distributed in Australia and throughout tropical Asia, America, Africa, Alaska (Copeland 1947; Lumpkin and Plucknett 1980; Tryon and Tryon 1982; Smith et al. 2006). Extant Marsileaceae is a small family (ca. 75 species) with three genera: the cosmopolitan *Marsilea* L. (ca. 70 species), *Pilularia* L. (5 species) found in western South America, and in temperate South America, Australia and New Zealand, and the monotypic *Regnellidium* Lindm. from Brazil, Uruguay, and Argentina (Kramer 1990; Zuloaga and Morrone 1996). The family Hydropteridaceae includes only fossils of *Hydropteris pinnata* Rothwell and Stockey from the Upper Cretaceous of western North America and combines the overall

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morphology of marsileaceous ferns with pinnate fronds like those of typical filiclean ferns (Rothwell and Stockey 1994). *Hydropteris* occupies a critical position in the phylogeny of heterosporous ferns and it incorporates features from Marsileaceae, Salviniaceae, and homosporous ferns (Nagalingum et al. 2006). The Hydropteridales are regarded by Smith et al. (2006) as part of the synonymy of Salviniaceae. Baluyeva (1964) described another critical taxon from the Upper Cretaceous of Russia, *Azinia paradoxa*, a fossil with some resemblance to Salviniaceae and Marsileaceae. Taylor et al. (2009) suggested placing *Azinia* in a separate family, Aziniaceae. Molecular and morphological analyses (Hasebe et al. 1995; Pryer et al. 1995, 2004; Pryer 1999) have shown *Azolla* as sister to *Salvinia*, forming a clade that is sister to the clade formed by the three genera within Marsileaceae (Metzgar et al. 2007). The three genera are easily distinguished by their leaf morphology, while *Marsilea* has four wedge-shaped leaflets in a cruciform arrangement and *Regnellidium* has two oppositely arranged leaflets, *Pilularia* is characterized by narrow filiform leaves (Nagalingum et al. 2008). Heterosporous ferns are characterized by heterospory (the production of mega and microspores) and by the distinctive reproductive structures traditionally known as “sporocarps” (Nagalingum et al. 2006). In a comparative morphological study of the reproductive structures in heterosporous water ferns, Nagalingum et al. (2006) redefined the term “sporocarp” as a sorophore and sori surrounded by a sorophore envelope. Following this definition they concluded that sporocarps occur in Marsileaceae and *Azolla* but not in *Salvinia* because the sorophore envelope is absent.

The fossil record of the family Salviniaceae is unusually rich with several genera and many species, and consists of vegetative remains, dispersed megaspores, and microspore massulae (Florin 1940; Taylor et al. 2009). In contrast, Marsileaceae are poorly represented in the fossil record (Lupia et al. 2000) and most marsileaceous fossils are known only from micro- and megaspores, whereas sporocarps and leaf macrofossils are relatively rare (Nagalingum 2007). The oldest fossils assignable to Marsileaceae include the disperse microspore *Crybelosporites berberioides* Burger from the Late Jurassic-Albian of the Falkland (Malvinas) Islands (Kotova 1983) and the whole plant *Regnellites nagashimae* Yamada and Kato from the Late Jurassic to earliest Early Cretaceous (Berriasian) of Japan (Yamada and Kato 2002). Marsileaceous macro- and mesofossils are most common in Late Cretaceous floras and include sporocarps and whole plants from India (Chitale and Paradkar 1972; Banerji 1987) and Japan (Yamada and Kato 2002). One sporocarp (Lupia et al. 2000) and two macrofossils (Skog and Dilcher 1992, 1994; Rich et al. 2001) were reported from North America. Other

than the fragments described from India (Banerji 1987), there are few macrofossils of Marsileaceae recorded from Gondwana. Nagalingum (2007) reported three marsileaceous macrofossil taxa from Antarctica and Australia, and Hu et al. (2008) described a species from the Africa/Arabian Peninsula. In South America, *Crybelosporites* has been recovered from Cretaceous sediments of Brazil and Peru (Brenner 1968; Herngreen 1973; De Lima 1982; De Lima et al. 1982). In Argentina, the oldest record is based on the occurrence of *Crybelosporites* cf. *berberioides* from the Berriasian-Barremian of the Springhill Formation, Tierra del Fuego, Argentina (Rebasa 1982; Cornú 1986). However, the presence of this family was confirmed by the occurrence of the microspore *Crybelosporites* associated with the megaspore *Arcellites* from the Albian Kachaike and Piedra Clavada formations outcropping at Santa Cruz Province (Archangelsky and Llorens 2005; Baldoni 1987; Baldoni and Taylor 1988; Batten et al. 1996; Baldoni et al. 2001; Del Fueyo et al. 2007; Villar de Seoane and Archangelsky 2008). The genus *Crybelosporites* has been recovered also from other Argentinean Cretaceous associations (e.g., Baldoni 1987, 1992; Archangelsky et al. 1994; Prámparo 1994; Prámparo et al. 2005). Recently, marsileaceous macro- and microfossils were collected from the Campanian–Maastrichtian mid-levels of the La Colonia Formation, Chubut, Argentina (Cúneo et al. 2013; Hermsen et al. 2014). Cúneo et al. (2013) described the fossil species *Regnellidium thomas-taylorii* Cúneo, Gandolfo et Hermsen that includes leaves, rhizomes, a putative sporocarp, and dispersed spores. Additionally, Hermsen et al. (2014) erected *Mirasolita irupensis* Hermsen, Gandolfo et Cúneo (leaves and leaflets), associated with *Lugiomarsiglia aquatica* Gandolfo, Hermsen et Cúneo (sporocarps) and spores. These fossils constitute the first macrofossils confidently assigned to Marsileaceae from South America. Interestingly, these fossils were found in sediments that contain the marsileaceous megaspores and microspores, *Molaspora lobata* (Dijkstra) Hall and *Crybelosporites*, respectively.

The aim of the present contribution was to report the finding of new fossil remains with marsileaceous affinities from the Late Cretaceous Loncoche Formation, Calmu-Co section, Northern Neuquén Basin, Mendoza, Argentina. Fossils are scattered leaflets, rhizomes, roots and a single sporocarp-like structure (previously published as *Salvinia* aff. *preauriculata* Berry by Alvarez-Ramis et al. 2004). They are assigned to the new taxon *Mendozaphyllum loncochensis* gen. and sp. nov. and compared to other marsileaceous macrofossils from the Cretaceous of Argentina. The new taxon is associated with dispersed microspores corresponding to *Crybelosporites*, different types of massulae of Salviniaceae, and a single megaspore of the fossil genus *Granelispora* all recovered from the

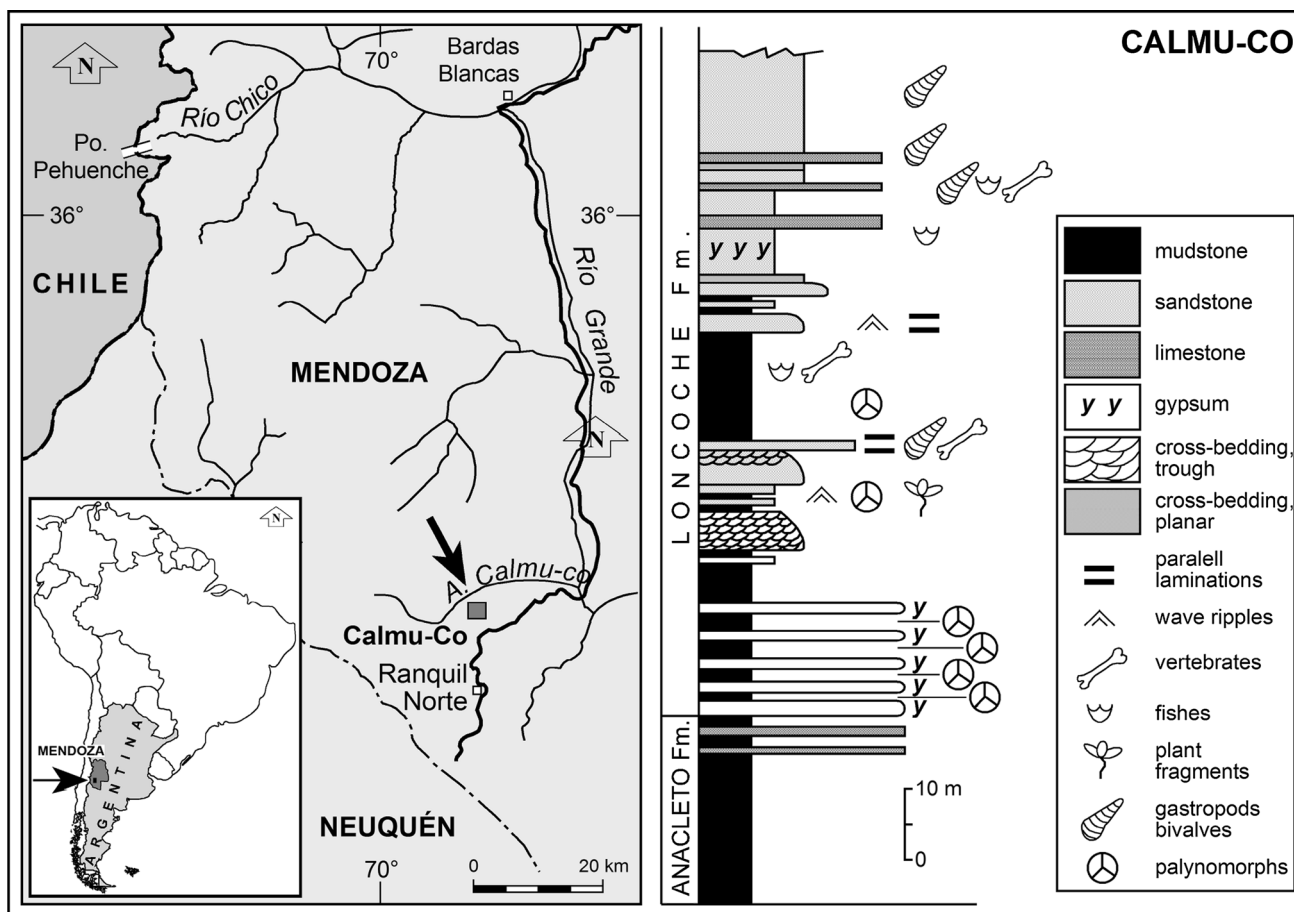


Fig. 1 Location map of the studied area (Calmu-Co) South of Mendoza Province, Argentina, and the stratigraphic section indicating the plant bearing horizon and palynological samples

same sediments. The fossil-genus *Crybelosporites* is reported for the first time in the Late Cretaceous palynological associations from the Malargüe Group.

Materials and methods

Geographic and stratigraphic context

The Loncoche Formation (Campanian to early Maastrichtian, Upper Cretaceous) is the basal unit of the Malargüe Group. The lower and middle part of this unit is well exposed at the Calmu-Co locality, located at 36°30'S, and 69°50'W, south of Mendoza Province (Fig. 1). In this section, the Loncoche Fm. is composed of clayey, silty, and sandy beds, with some gypsum and marls interbedded, integrated into four depositional facies associations (Parras et al. 2001; Previtera and González Riga 2008). In the northernmost exposure of the Neuquén Basin west of the town of Malargüe, southern Mendoza Province, Upper Cretaceous sediments accumulated in a narrow embayment

of ~120 km wide in a retroarc position, according to regional mapping survey (Uliana and Biddle 1988; Legarreta et al. 1989; Nández and Malumián 2008), which records the initial connection of the Neuquén Basin to the Atlantic Ocean. In the Calmu-Co area, the fossil record shows less marine influence compared to the other outcrops of the basin. Parras et al. (1998) and Parras and Griffin (2013) interpreted the depositional environment of the area (south of Mendoza) as fluvial to deltaic, with a few lacustrine episodes under a sporadic marine influence, for the lower and middle part of the Loncoche Fm. In the middle part of the Calmu-Co section, diverse vertebrate remains were collected including fishes (Teleostei, Lepisosteidae and Dipnoi), turtles, elasmosaurid plesiosaurs, and titanosaurs and theropods dinosaurs (Previtera and González Riga 2008; Previtera 2013). Vertebrate remains are preserved in parautochthonous–allochthonous concentrations of clastic and calcareous facies (bioclastic sandstone composed of mollusks) that are interpreted as channel and deltaic plain environments by Previtera and González Riga (2008). An invertebrate macrofauna was also recovered

from the lower and middle sections and consists of bivalves and gastropods indicative of freshwater to restricted marine environments (Parras and Griffin 2013).

The plant macrofossils and palynomorphs described herein were collected from the fine-grained sediments corresponding to the lower to middle part of the formation (Fig. 1). Macrofossils are preserved as impressions, but unfortunately they are fragmented and lacking cuticles. Nevertheless, numerous scattered leaflets, rhizomes, and roots were recovered in association with diverse fragments belonging to different groups of plants (Álvarez Ramis et al. 2004). Six samples were taken for palynological studies from the base to the middle part of the outcropping section (fine grain lithologies) including one sample obtained solely from the bearing plant layer (Fig. 1).

Specimen curation, preparation, and documentation

The examined plant macrofossils are housed at the Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA), Centro Científico Tecnológico (CCT-CONICET), Mendoza, Argentina, under the catalog/collection numbers IANIGLA-PB: 001-011. The description herein presented is based on all 11 specimens. They were studied using light stereomicroscope and photographed with Olympus SP 350 digital camera. Herbarium specimen of extant fern figured for comparative purpose is from the collections of the L. H. Bailey Hortorium Herbarium (BH, Department of Plant Biology, Cornell University, Ithaca, New York, USA).

Palynological samples were processed using standard techniques, with HF and HCl (Volkheimer and Melendi 1976). No oxidation was needed. The residues were sieved on 10 and 150 µm mesh nylon filter, stained with Safranin, and mounted in glycerin jelly. Four slides were studied of each fraction (>150 and 10–150 µm). *Grappelispora* and diverse massulae were recovered from the >150 µm fraction. The samples were examined with a light microscope (Olympus BX50) and photographed with a digital camera mounted on the microscope. England Finder coordinates are provided for the illustrated specimens. All the resulting samples are stored in the paleopalynological collection of the Unidad de Paleopalynología, Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA, CCT-CONICET-Mendoza) under the catalog numbers MPLP: CAL1 (9351), CAL2 (9352), CAL3 (9353), CAL4 (9354), CAL5 (9355), CAL5' (9356), CAL6 (9357), CAL (10137).

Systematics

Order Salviniales Bartling

Family Marsileaceae Mirbel

Fig. 2 *Mendozaphyllum loncochense* Puebla, Prámparo & Gandolfo, sp. nov. **a** A single leaflet with a rhizome showing dichotomously open venation and a sporocarp-like structure. IANIGLA-PB 005. **b** Details of the leaf epidermal characters. **c** Details of a sporocarp-like structure. **d** Petiolate leaflet and folded leaflet (*bottom left*). IANIGLA-PB 006. **e** Leaves; a leaf fragment with three leaflets (*top right corner*) and isolated leaflets. IANIGLA-PB 001, 002, 003. **f** Single leaflet showing lamina shape and dichotomously open venation pattern. IANIGLA-PB 004. **g** Line drawings based on IANIGLA-PB 004. **h** *Mirasolita* leaflets from the La Colonia Formation. IMG_1902: MPEF-Pb 5520. **i** Line drawings based on IMG-1902: MPEF-Pb 5520. **j** Leaflets of *Regnellidium thomastaylorii* MPEF-Pb 5446. **k** Line drawings based on MPEF-Pb 5446. Scale bars **a–d, h, i** 0.5 mm; **e, j–k** 10 mm; **f, g** 2.5 mm

Genus *Mendozaphyllum* Puebla, Prámparo & Gandolfo, gen. nov.

Generic diagnosis. Plant with rhizome, roots, and compound leaves; rhizome bearing roots ventrally and leaves dorsally, leaves with two or four glabrous leaflets; petiolule present, leaflets cuneate to obovate in shape, apex entire to crenate, base straight to convex, dichotomously open venation, lacking anastomoses and marginal vein.

Type species here designated. *Mendozaphyllum loncochense* Puebla, Prámparo & Gandolfo, sp. nov.

Etymology. The generic name refers to Mendoza Province where the Loncoche Formation outcrops. The specific epithet refers to the Loncoche Formation where the fossils were collected.

Holotype here designated. IANIGLA-PB 011, (Fig. 3b).

Paratypes. IANIGLA-PB 001-010, (Fig. 2a–f).

Type locality. Depositional facies B of the basalmost Calmu-Co section of the Loncoche Formation.

Stratigraphic occurrence and age. Depositional facies B of the basalmost Calmu-Co section of the Loncoche Formation, Campanian–Maastrichtian, Upper Cretaceous.

Species description. The plants are composed of rhizomes bearing roots and leaves. The largest and most complete plant consists of a rhizome fragment (2.5 cm long and 4 cm wide) bearing numerous roots (Figs. 2a, c, 3b) on its ventral side and leaflets on the dorsal side. The leaflets are borne at the top of a long petiole, 2 cm long and 1 mm wide (Fig. 3b). Each leaflet has a tapering proximal region and a short petiolule. In general, these structures can be observed at isolated leaflets that share common morphological features. All leaflets are small, but their shape and size are slightly variable, 3–6.5 mm long and 2.5–6.5 mm wide. Overall, the leaflets shape is cuneate to obovate, and their margin at the base is straight to convex while at the apex is entire to crenate (Figs. 2a, d–f, 3b). The venation is dichotomously open and does not have anastomoses or they are not preserved, and there is no marginal vein or it is not preserved. The preservation of the fossils allows the recognition of few leaf epidermal characters. Epidermal cells

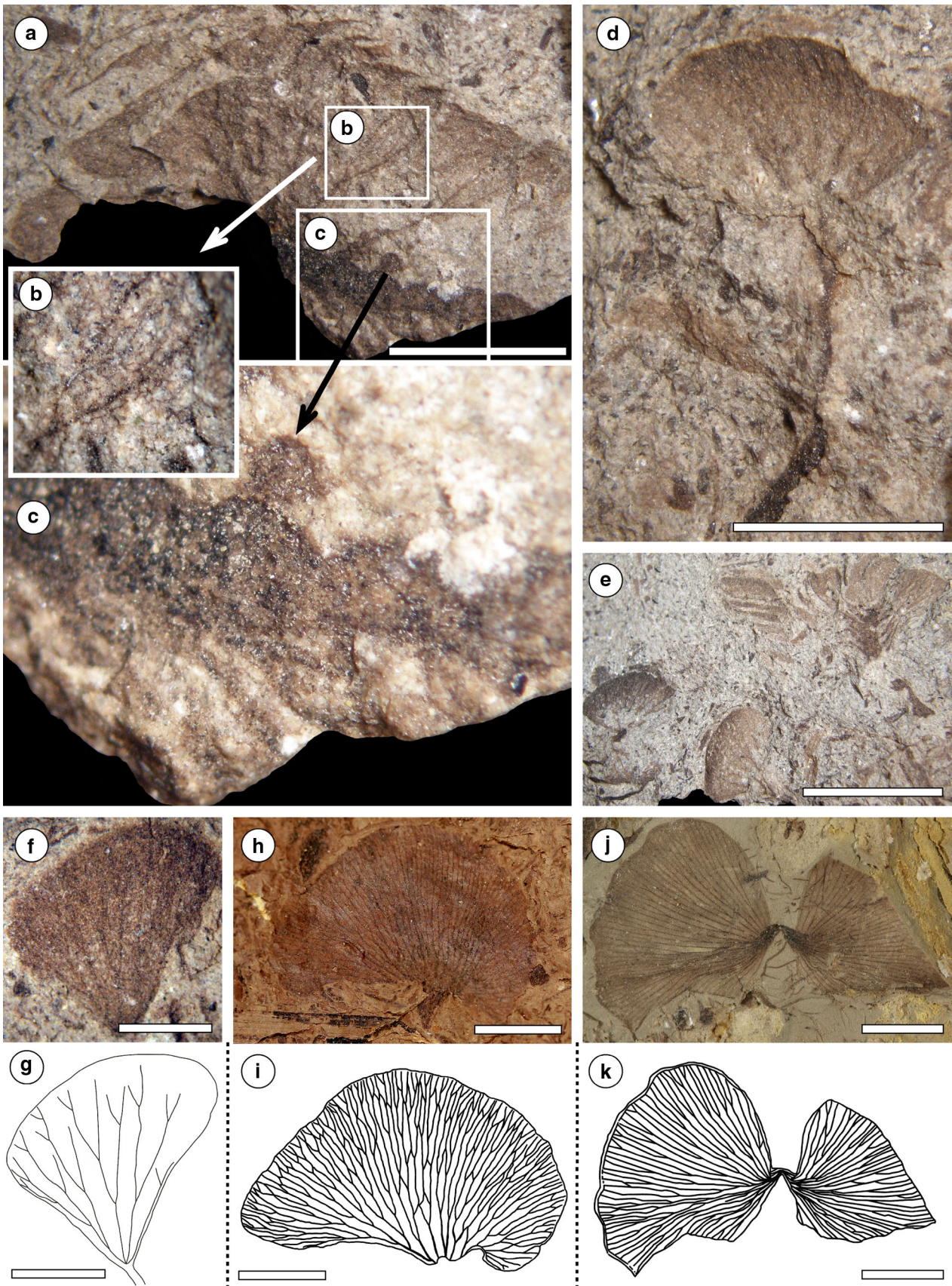
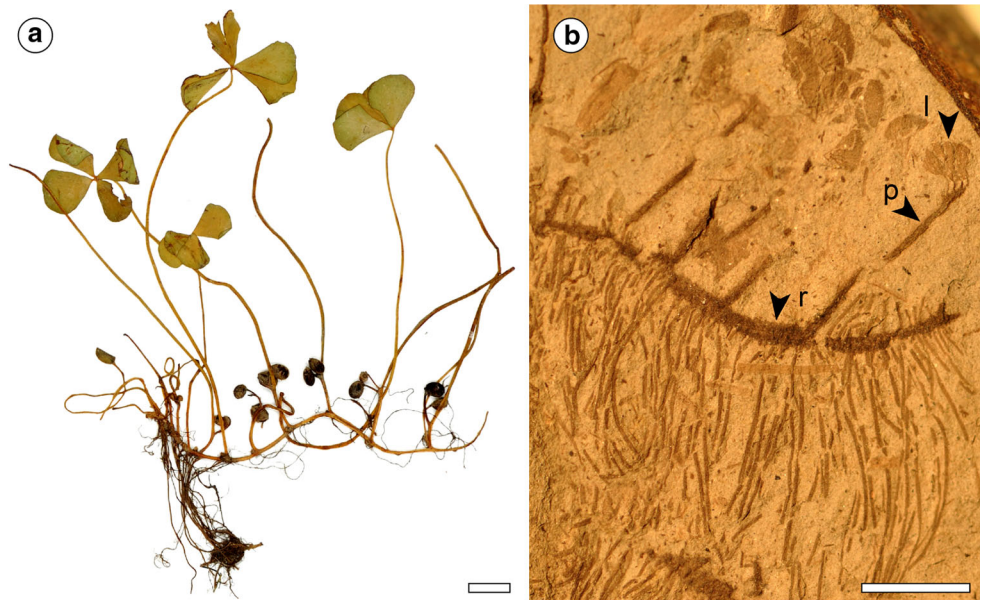


Fig. 3 **a** *Marsilea quadrifolia* L. Herbarium specimen showing leaves, sporocarps, and roots attached to a horizontal rhizome. BH 000 050 804 **b** *Mendozaphyllum loncochense* Puebla, Prámparo & Gandolfo, sp. nov. Specimen showing petiolated leaves (l: leaf, p: petiole), rhizome (r: rhizome) and branched root system. Holotype. IANIGLA-PB 011. Scale bars **a**, **b** 1 cm



are polygonal; however, those adjacent to the veins are more elongated and fusiform (Fig. 2b). It is difficult to distinguish the exact number of leaflets that formed the leaves; however, it seems to be two or four leaflets. It is clear that the leaflets are overlapping, probably as a consequence of the taphonomic process.

Only one of the specimens (Fig. 2a–c) shows a sporocarp-like structure attached to the rhizome near the base of a leaf-stalk. The sporocarp-like structure is 0.5 mm long by 0.6 mm wide, short-stalked, and bean-shaped (Fig. 2c).

Comments. The fossils herein described are morphologically similar to extant Marsileaceae and they fit perfectly within the diagnosis for marsileaceous vegetative organs (Kramer 1990; Nagalingum et al. 2006). The leaves of the fossil species resemble those of living Marsileaceae in their general shape, open dichotomous venation, and lack of a prominent midvein. The Loncoche fossils are very distinctive from *Pilularia*. *Pilularia* does not produce leaflets. However, the fossils of the Loncoche Fm. are similar to those of *Marsilea* and *Regnellidium* because the Loncoche leaves are composed of two or four leaflets. Some of the morphological characters (such as absence of midveins, dichotomously open venation, two or four leaflets) observed in the fossils suggest affinities to extant *Marsilea*; nevertheless, the fossil remains lack characters unique to extant *Marsilea*, and, therefore, they cannot be placed with certainty within the extant genus.

After considering all the characters observed in the fossil remains, clearly the Loncoche marsileaceous fossils cannot be included into any marsileaceous fossil-taxa previously described (see “Discussion” below).

Fig. 4 Palynological association from Calmu-Co section, Loncoche Formation. *Crybelosporites pannuceus* (Brenner) Srivastava (1977). **a**, **b** (9352A:X40). **a** Proximal view showing the trilete mark. **b** Distal view. **c** 9352 A lateral equatorial view showing the acrolamella in the proximal pole (top right), **d** (9352D:F32/1), **e** (9352E:J21), **f** (9352A:J39/2), **d–f** Different specimens showing variations in the rugulo-reticulate sculpture and the modifications of the perine to form the acrolamella. **h–g** *Grapnelispora loncochense* Papú. (10137D:T18 ½). **h** General view of the specimen with a broken upper process. **g** Details of a bifurcate appendage with grapnel-like tips. **i–j** *Paleoazolla patagonica* Archangelsky, Phipps, Taylor and Taylor. (10137F:M40). **j** Massulae with glochidia; **i** Details of the multi-barbed glochidia with recurved barbs. **k–m** *Azolla circinata* Oltz and Hall in Hall. **k** (9353C:E31/3), Oval massulae with one circular microspore and the characteristic coiled glochidia. **m**, **l** (9353C: O28), **m** Two circular massulae. **l** Details of the coiled glochidia in the massulae, one of it indicated with an arrow shows a 3-µm enlarged base. **n** (9353B:M27/0) Detail of the coiled glochidia which terminate in spherical knobs. Scale bars **a–f**, **g**, **i**, **k–n** 10 µm; **h**, **j** 20 µm

Associated palynoflora

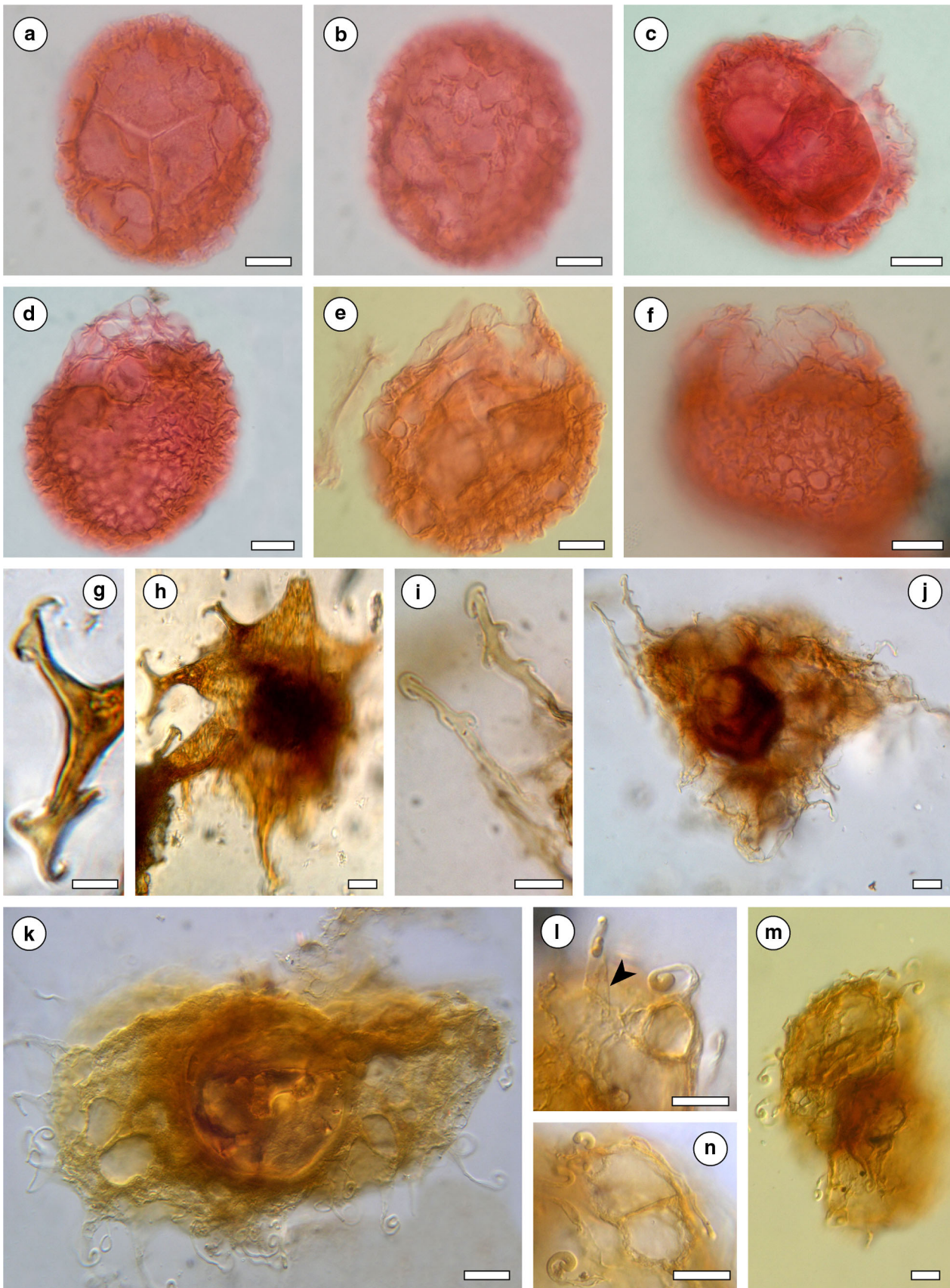
In all the samples studied from the Calmu-Co section, abundant and very well-preserved dispersed spores belonging to the fossil spore-genus *Crybelosporites* were found. Also, a single megaspore assigned to *Grappnelispora loncochensis* was recognized.

Microspores

Genus *Crybelosporites* Dettmann

Type species *Crybelosporites striatus* (Cookson and Dettmann) Dettmann (1963)

Crybelosporites pannuceus (Brenner) Srivastava (1975), Fig. 4a–f



Remarks. The specimens from the Loncoche Formation have a circular amb, with rugulo-reticulate perine, modified at the proximal pole and forming an acrolamella. The perine that it is 3–7 μm thick, is ornamented with an irregular reticulum composed of membranous sinuous muri that enclose polygonal to irregular lumina; the lumina are between 3–5 μm in diameter. Instead of being reticulate, in some specimens, the perine is ornamented by irregular folds that give the spores a highly wrinkled aspect (Fig. 4c, e). The laesurae are straight, extending $\frac{3}{4}$ of the spore radius, and they are best seen in polar view (Fig. 4a) and in equatorial view when the rays of the trilete mark are open (Fig. 4c, f). The inner layer (central body) is smooth, and 1.5–2 μm thick.

Dimensions. Equatorial diameter: 37–50 μm ; polar diameter: 42–60 μm included the acrolamella; diameter of inner layer: 35–45 μm (30 specimens).

Comparisons. *Crybelosporites striatus* described by Dettmann (1963) is mainly characterized by a proximal striate and distally and equatorially reticulate perine, with straight laesurae, length $\frac{3}{4}$ spore radius with weakly thickened lips and equatorial diameter of 28–45 μm . *Crybelosporites striatus* and *C. pannuceus* are very similar in morphology following the original diagnosis; the only difference seems to be the larger spore dimensions, a thicker inner layer in *C. pannuceus*, and the presence of lips in *C. striatus*. The specimens from the Loncoche Formation are most similar to *C. pannuceus* following these criteria. *Crybelosporites berberioides* Burger (1976) is frequently found in tetrahedral tetrads, with the outer wall arranged into loose folds showing a rugulate zig-zag pattern distally. We found only individual specimens in the studied samples. *Crybelosporites brenneri* Playford (1971) from the Lower Cretaceous of Canada has stratified sclerine with a very thin outer layer about 0.5 μm thick that is in close proximity to the inner layer around the distal surface and equator, and the sculpting very fine sculptured (scabrate to microrugulate). The thin and very fine ornamented perine distinguishes *C. brenneri* from *C. pannuceus*. *Crybelosporites australis* Archangelsky and Llorens (2005), the only species known in Argentina from the Albian, Kachaiké Formation, Austral Basin, is different from *C. pannuceus* because of the variable ornamentation of the perine, from irregular reticulate (1–2 μm) microreticulate to micropunctate. Specimens of *C. australis* were found by Villar de Seoane and Archangelsky (2008) among the appendages of the megaspore *Arcellites santacruzensis* Baldoni (1987) in samples from the Kachaiké and Piedra Clavada Formations.

Distribution. *Crybelosporites* is a significant genus for Lower Cretaceous biostratigraphy worldwide. It appeared in the Late Jurassic but increases in frequency and diversity during the Barremian to the Cenomanian (Srivastava

1978). However, its Late Cretaceous record is scarce. Lupia et al. (2000) gave a complete synopsis of its stratigraphic range worldwide. In Argentina, *Crybelosporites* is well known from different Lower Cretaceous palynofloras (for its complete distribution see Hermsen et al. 2014).

Crybelosporites is not often mentioned in Late Cretaceous palynofloras. There are only two records so far for this genus from the Late Cretaceous in Argentina. Baldoni (1992) described only one specimen assigned to *Crybelosporites* sp. for the Maastrichtian Lefipán Formation, Chubut Province, but unfortunately it is not well illustrated. Recently, Cúneo et al. (2013) described and illustrated dispersed microspores of *Crybelosporites* from the Campanian–Maastrichtian sediments of the La Colonia Formation, also from the Chubut Province. These microspores were found in association with macrofossils assigned to *Regnellidium* and with *Molaspora* megaspores. The La Colonia microspores assigned to *Crybelosporites* cf. *pannuceus* (Brenner) Srivastava (Cúneo et al. 2013; Fig. 4d, e) are very similar in dimensions and ornamentation to the specimens herein described.

Boltenhagen (1967) erected the genus *Gabonispuris* for trilete perinate spores lacking acrolamellae and with a dense sculpture of bacula. Subsequently, Srivastava (1972) proposed to restrict this genus to include only perinate spores possessing setaceous, funnel-shaped or papillose processes on the perine. *Gabonispuris* is very common in Late Cretaceous associations and was considered also to represent dispersed Marsileaceae spores. Some specimens misidentified in the literature as *Gabonispuris* could be *Crybelosporites*, expanding its distribution into the Late Cretaceous.

Megaspores

In association with *Mendozaphyllum loncochense* and from the bearing plant layer, a single megaspore assignable to *Granelispora loncochensis* Papú (1997) (Fig. 4g–h) was recovered. *Granelispora loncochensis* was first described from the lower part of the Loncoche Formation, Ranquil-Co locality, southern Mendoza (Papú 1997). Its presence was documented in other palynofloras from the Late Cretaceous (late Campanian–Maastrichtian) of Northern Patagonia (Allen, Jagüel, Angostura Colorada, and Paso del Sapo formations), the Austral Basin (Calafate Formation), and Antarctica (Lopez Bertodano Formation) (Palamarczuk and Gamero 1988; Sepúlveda et al. 1989; Papú 1997, 2002; Marensi et al. 2004; Vallati 2010). There are no records of *G. loncochensis* in Paleogene associations in Argentina. *Granelispora loncochensis* is characterized by the presence of glochidia (appendages).

The anchor shape of the glochidia is considered to be an adaptive morphological character related to heterosporous

ferns (Papú 1997) but taxonomic affinities of *Granelispora* are still unknown. This megaspore has never been found in organic connection with any vegetative or reproductive structures. Remarkably, this is the first report of *Granelispora* in association with aquatic fern fossil remains. Archangelsky et al. (1999) observed that *G. loncochensis* and *Paleozolla patagonica* Archangelsky et al. (1999) have almost identical glochidia, on the megaspore and on the massulae, respectively. However, after comparing the morphological characters of both taxa (such as size and shape of megaspore and massulae, wall structure and ornamentation, etc.), Archangelsky et al. (1999) concluded that they are very different and proposed that the similarities of the anchoring systems are due to parallel evolution, rather than homology. Unfortunately, the affinities of *Granelispora* will remain unresolved until the megaspores appear in association with reproductive or any other diagnostic vegetative remain.

Massulae

The palynoflora of the Calmu-Co locality also produced abundant isolated massulae of Salviniaceae, the other aquatic fern family. Among them, triangular massulae (180 µm high) with multi-barbed anchor-shaped glochidia and indeterminate spores (of 47 µm in diameter) (Fig. 4i, j) were recognized. These massulae are similar in morphology, shape and size, and with the glochidia of the original material described by Archangelsky et al. (1999) as *Paleozolla patagonica* from the La Colonia Formation. Oval to circular (60–150 µm) massulae, with sparsely spaced coiled glochidia, most of which terminate in spherical knobs (Fig. 4k–m), were also encountered in the Calmu-Co palynological association. The glochidia of these massulae are aseptate, 1–3 µm in diameter at the base, and 15–25 µm long; the microspores are circular with a diameter of 28–30 µm. These massulae are comparable to *Azolla circinata* Oltz and Hall in (1968). Both taxa are members of the other aquatic fern family Salviniaceae. Significantly, Papú (2002) reported, in the only published palynological association from the Calmu-Co locality, the presence of *Azolla cretacea* Stanley, *Azolla (Rhizosperma)* sp. and *Azollopsis polyancyra* (Stough) Sweet and Hills; and although these taxa were not found in the present study, their record is indicative of the great diversity of aquatic ferns in the Loncoche Formation association.

Discussion

In a preliminary report on the Loncoche macroflora collected at the Calmu-Co section, Álvarez Ramis et al. (2004) assigned the small leaflets, herein described, to *Salvinia* aff.

preauriculata Berry. However, the leaflets from Calmu-Co do not exhibit the morphological characters (such as size, shape, venation pattern, and arrangement of the leaflets) typical of the genus *Salvinia*, and, therefore, they cannot be placed within *Salvinia* or the family Salviniaceae as suggested by Álvarez Ramis et al. (2004).

Based on the observed characters in the fossils herein described, it is clear that the macrofossils from Loncoche Formation are morphologically similar to members of Marsileaceae, and certainly they correspond to the emended diagnosis for marsileaceous vegetative organs as defined by Hermsen et al. (2014). Nagalingum (2007) proposed the use of the fossil-taxon *Marsileaceaeophyllum* for sterile whole plants, detached leaves, and leaflets that are similar to extant *Marsilea*. Nevertheless, Hermsen et al. (2014) emended the generic diagnosis of *Marsileaceaeophyllum*, making it clear that this fossil genus only includes remains that have leaves and leaflets with vein architecture similar to extant *Marsilea* but lack reproductive structures (sporocarps and spores). Based on the new diagnosis, only leaves with four leaflets, and leaflets with dichotomous venation with few anastomoses and a marginal vein can be considered as belonging to *Marsileaceaeophyllum*. *Mendozaphyllum* is characterized for having leaflets attached to a long petiole, and dichotomous open venation pattern, lacking anastomoses and no marginal vein, so it cannot be placed within *Marsileaceaeophyllum*. In addition, Hermsen et al. (2014) only recognized two species of *Marsileaceaeophyllum*, *M. johnhallii*, and *M. campanicum*. Although *Mendozaphyllum loncochense* shares some morphological characters with these species such as the open dichotomous venation, the shape of the leaflets, and the margin type, the veins of *M. loncochense* do not anastomose and lack marginal vein, distinguishing *M. loncochense* from *Marsileaceaeophyllum* species, in which veins anastomosed and have a marginal vein.

Recently, two Marsileaceae species from the Cretaceous of Argentina have been described constituting the first reports on macrofossil in association with reproductive structures for the family in the Southern Hemisphere (Cúneo et al. 2013; Hermsen et al. 2014). These species come from three localities of the La Colonia Formation (Cañadón del Irupé, Cerro Bosta, and Quebrada del Helecho), Chubut Province, Argentina. *Regnellidium thomas-taylorii* Cúneo, Gandolfo et Hermsen from the Quebrada del Helecho and Cerro Bosta localities, includes leaves with two leaflets, rhizomes with numerous roots, putative sporocarps, and dispersed spores obtained from the same sediments (Cúneo et al. 2013). *Mendozaphyllum loncochense* has a combination of characters that clearly distinguishes it from *R. thomas-taylorii*. The two species differ in size (*M. loncochense* is smaller than *R. thomas-taylorii*), and shape and number of leaflets (*R. thomas-taylorii* has two cuneate to flabellate

leaflets while the ones of *M. loncochense* has up to four cuneate to obovate leaflets). Although both species have dichotomous venation, they differ in that *R. thomas-taylorii* has few anastomoses and a strong marginal vein while in *M. loncochense* the venation pattern is open dichotomous, without a marginal vein and does not have anastomoses (Fig. 2j, k). *Mirasolita irupensis*, from the Cañadón del Irupé locality, is most similar to living species of *Marsilea* (Hermsen et al. 2014). *Mirasolita* leaves have at least two leaflets, obovate with a concavo-convex and decurrent base and present dichotomous venation with anastomoses throughout the lamina; the anastomoses form elongate areoles that become shorter toward the apex, and a delicate marginal vein. Some of these characteristics are shared with *M. loncochense* but the species differ in size, shape and venation type (Fig. 2h, i). The Calmu-Co fossils are quite different from these two Patagonian fossils Marsileaceae, making their inclusion within any of them incorrect; therefore, a new species, *Mendozaphyllum loncochense*, is erected.

Mendozaphyllum loncochense was recovered from sediments that yield a rich palynological association of aquatic ferns. *Mendozaphyllum loncochense* macrofossils were found in the same sediments that produced disperse marsileaceous microspores (*Crybelosporites pannuceus*) and the megaspore (*Grapnelispora loncochensis*). Although the macro- and microfossils were not found in organic connection, the fact that they were collected from the same sediments confirms the presence of the family and supports the assignment of the fossils within the family. Additionally, the presence of abundant *C. pannuceus* also suggests the possibility that these spores were probably produced by *M. loncochense*.

Modern Salviniaceae are free-floating aquatic plants living on the surface of fresh waters while modern Marsileaceae are rhizomatous plants rooted in substrates of shallow waters and whose petioles extend to the water surface on which the lamina may rest (Collinson et al. 2013). Sedimentological data indicate that the paleoenvironment for the lower and middle part of the Calmu-Co section of the Loncoche Formation is fluvial to deltaic, with lacustrine episodes (Previtera and González Riga 2008; Previtera 2013; Parras and Griffin 2013). This interpretation is also supported by the diverse invertebrate and vertebrate fossil fauna (fresh water mollusks, fishes, turtles) and by the abundant fresh water algae (*Botryococcus*, *Pediastrum* and zygnematacean algae) recovered from the palynological association (Prámparo pers. comm.). This was probably the optimum habitat for the growth of aquatic ferns related to Marsileaceae and Salviniaceae, and explains its abundance in the studied sediments.

The genus *Grapnelispora*, which comprises two species (*G. evansii* and *G. loncochensis*), has a paleogeographic

distribution restricted to Patagonia, Argentina (Sepúlveda et al. 1989; Papú 1993, 1997; Marensi et al. 2004; Vallati 2010; Barreda et al. 2012), Antarctica (Askin 1990; Palamarczuk and Gamarro 1988), and the Austral-Papuan region (Stover and Partridge 1984). In Campanian and Maastrichtian sediments from New Zealand, *G. evansii* is used as a marker species for the Cretaceous–Paleogene boundary where it goes extinct above the K–Pg boundary clay (Vajda et al. 2001; Vajda and Raine 2003, 2010). As it is not present in latest Maastrichtian–Paleocene associations of Argentina, Prámparo (2012) suggested that *G. loncochensis* is a good marker of the late Campanian–early Maastrichtian continental palynofloras at least for the Neuquén Basin. Its presence in the Calmu-Co section of the Loncoche Formation corroborates at least a Campanian–Maastrichtian age for the section.

Concluding remarks

In summary, the presence of fossil Marsileaceae in the Campanian–Maastrichtian Loncoche Formation, Mendoza, is confirmed by the presence of vegetative (*Mendozaphyllum loncochense*) and reproductive (the microspores *Crybelosporites pannuceus*) remains. Noteworthy, it is the occurrence in the same sediments of the megaspore *Grapnelispora loncochensis* and abundant isolated massulae from different species of aquatic ferns, which confirms the close affinity of *Grapnelispora* to the aquatic ferns as previously suggested by Papú (1997) and supports the possibility that this megaspore might be related to the aquatic ferns. These records extend towards the north the paleogeographical distribution of marsileaceous affinity aquatic ferns in Argentina, since previous records are from Patagonia.

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