

New marsileaceous fossils from the Late Cretaceous of South America and a reevaluation of *Marsileaceaphyllum*

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Abstract Herein we report new macrofossils and associated microfossils representing the aquatic fern family Marsileaceae from the Campanian to Maastrichtian Cañadón del Irupé locality, La Colonia Formation, Chubut Province, Argentina. The macrofossils include compound leaves, detached leaflets, and sporocarps. The venation of the leaflets is consistent with the diagnosis of *Marsileaceaphyllum*, which we argue is poorly defined. Consequently, the circumscription and diagnosis of *Marsileaceaphyllum* are emended in order to limit the taxon to include only leaves or rhizomes bearing leaves with four leaflets that most resemble those of *Marsilea* among extant genera of Marsileaceae. The Cañadón del Irupé leaves and leaflets are assigned to the new genus *Mirasolita*, erected to encompass compound leaves bearing two petiolulate leaflets, each leaflet having a reniform lamina and reticulate venation. The architecture of *Mirasolita* leaves and leaflets is distinct from that of leaves of any of the living marsileaceous genera. The stalked sporocarps are assigned to the new genus *Lugiomarsiglia*. They are attributed to Marsileaceae because each has a sclerenchymatous wall surrounding circular bodies interpreted as sporangia. Associated megaspores are assigned to

Molaspora lobata, a geographically widespread, primarily Late Cretaceous dispersed spore taxon. The co-occurrence of *Molaspora lobata* with an extinct marsileaceous leaf form fits a pattern wherein Cretaceous *Regnellidium*-like megaspores are associated with or found in situ within marsileaceous macrofossils that display a variety of morphologies.

Keywords Cretaceous · fossil · La Colonia Formation · Marsileaceae · Patagonia

Introduction

Marsileaceae Mirb. are rhizomatous, semi-aquatic ferns, living examples of which are divided into three morphologically distinct genera: *Marsilea* L., *Pilularia* L., and *Regnellidium* Lindman (Tryon and Tryon 1982; Kramer 1990). Along with their sister clade, comprised of the floating aquatic ferns *Azolla* Lam. and *Salvinia* Séguier of the family Salviniaceae Martinov and the extinct monotypic family Hydropteridaceae Rothwell & Stockey (including only *Hydropteris pinnata* Rothwell & Stockey), they constitute the Salviniales Link, the order that includes the only known heterosporous leptosporangiate ferns (Smith et al. 2006, modified to include the extinct family after Rothwell and Stockey 1994 and Rothwell 1999). The family is widespread today, with *Marsilea* occurring on all continents but Antarctica and *Pilularia* found in North and South America, Europe and westernmost Asia, and Australasia (Tryon and Tryon 1982); *Regnellidium* is endemic to a small area in eastern South America (Alonso Paz and Bassagoda 2002). The record of fossils with putative affinities to Marsileaceae is long and well documented, extending from the Late Jurassic or earliest Early

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Cretaceous to recent worldwide (Lupia et al. 2000; Yamada and Kato 2002); it is primarily known from Cretaceous occurrences of dispersed microspores (*Crybelosporites* Dettmann) and megaspores (*Molaspora* Schemel emend. Hall and possibly *Arcellites* Miner emend. Ellis & Tschudy) (Collinson 1991, 1996; Lupia et al. 2000; Batten et al. 2011). Despite this, the evolutionary history of Marsileaceae remains enigmatic, in part due to the fragmentary macrofossil record of the family and the difficulties posed in untangling the affinities of the extinct dispersed spore forms (e.g., *Arcellites*) to the extant and macrofossil taxa.

Within Marsileaceae, the species-rich *Marsilea* clade is consistently recovered as sister to a clade composed of the smaller genus *Pilularia* and its sister species *Regnellidium diphylum* Lindman in phylogenetic analyses (Rothwell and Stockey 1994; Hasebe et al. 1995; Pryer 1999; Rothwell 1999; Nagalingum et al. 2008). Each extant genus can be identified on the basis of its characteristic leaf architecture. *Pilularia* has filiform leaves, whereas *Regnellidium* and *Marsilea* have compound leaves with leaflets borne oppositely or in a pseudowhorl, respectively, at the apex of the petiole (Gupta 1962; Johnson 1986; Tryon and Tryon 1982; Kramer 1990; Pryer and Hearn 2009). *Regnellidium* has two broad leaflets with dichotomizing veins that anastomose infrequently (Pray 1962; Nagalingum 2007; Cúneo et al. 2013), whereas *Marsilea* has four narrower, obovate to obdeltoid leaflets with reticulate venation (Gaudet 1964; Johnson 1986; Nagalingum 2007). A variety of Cretaceous and Paleogene fossil leaf and leaflet forms similar to or with combinations of characters found in extant *Marsilea* and *Regnellidium* have been described (summarized by Nagalingum 2007 and Hu et al. 2008; additional descriptions by Fedotov 1978; Herman and Kvaček 2010; Cúneo et al. 2013). Until 2007, most reports of these leaves or leaflets (sometimes attached to other organs) were assigned to or considered comparable to *Marsilea* (Krasser 1906; Krasser, pers. comm. to Seward, in Seward 1910; Banerji 1987; Skog and Dilcher 1992, 1994; Rich et al. 2001; Kvaček and Herman 2004; Herman and Kvaček 2007), with a single species assigned to *Regnellidium* (Fedotov 1978), and rhizomes bearing sporocarps and leaves with two leaflets assigned to the genus *Regnellites* Yamada & Kato (Yamada and Kato 2002).

Collinson (1996, discussing the fossil taxon “*Marsilea*” *johnhallii* J. Skog & Dilcher) and Nagalingum (2007) have argued that the vegetative characteristics of the sporophyte alone are insufficient to determine the correct generic assignment for marsileaceous macrofossils, and that discovery of sporophytes bearing reproductive organs (i.e., sporocarps, ideally with in situ spores) is critical for unequivocal identification to genus. Thus, Nagalingum (2007) erected the new genus *Marsileaceaphyllum* to

encompass all fossils representing vegetative organs not attached to reproductive structures and exhibiting characteristics consistent with placement in Marsileaceae. To date, seven species and morphotypes of *Marsileaceaphyllum* have been recognized spanning the late Early Cretaceous (Albian) to Eocene (Nagalingum 2007; Hu et al. 2008; Herman and Kvaček 2010), including three occurrences that were identified as *Marsilea* prior to the establishment of the new fossil genus (see Nagalingum 2007; Herman and Kvaček 2010).

While the creation of *Marsileaceaphyllum* to encompass fossil marsileaceous vegetative organs with uncertain intrafamilial affinities was based on sound reasoning, the concept and application of the genus *Marsileaceaphyllum* have been problematic from the beginning. The diagnosis of the taxon (Nagalingum 2007: 44) relies on a priori assignment of fossils to Marsileaceae for application, except where they retain diagnostic leaflet venation. Leaflet venation characters highlighted in the generic diagnosis and succeeding discussion of *Marsileaceaphyllum* are not diagnostic exclusively for Marsileaceae, however, as leaflets consistent with the form taxon have been found attached to the *Hydropteris pinnata* plant. *Hydropteris* Rothwell & Stockey leaflets display a combination of *Marsilea*-like and *Regnellidium*-like venation characteristics, except that leaflets of *Hydropteris* lack marginal veins (Rothwell and Stockey 1994), as can leaflets assigned to *Marsileaceaphyllum* (Nagalingum 2007). *Hydropteris* is resolved as an extinct sister taxon to Salviniaceae in phylogenetic analyses (Rothwell and Stockey 1994; Pryer 1999; Rothwell 1999). Additionally, the name *Marsileaceaphyllum* has been inconsistently applied. For example, *Marsileaceaphyllum* has not been used as the genus for fossil leaves similar to *Regnellidium* (Cúneo et al. 2013), although Nagalingum (2007) indicated that *Marsileaceaphyllum* also encompasses these leaves. Finally, in our opinion, the taxon is overly broad because it obscures boundaries among the diagnostic leaf morphologies of the extant genera, as well as any novel forms that may be found in the fossil record.

In this contribution, we describe new fossil marsileaceous material from the Cañadón del Irupé locality (Fig. 1) of the La Colonia Formation, Chubut Province, Argentina. The remains include leaves and leaflets, associated (but not attached) sporocarps, and dispersed spores that we attribute to Marsileaceae. These specimens represent the first macrofossil occurrence of leaflets with *Marsilea*-like venation and the only unequivocal record of marsileaceous sporocarps from South America. The leaf and leaflet remains are consistent with the original concept of the genus *Marsileaceaphyllum* as described by Nagalingum (2007). Due to the problematic nature of the original concept of the genus, however, we provide an emendation that excludes the new

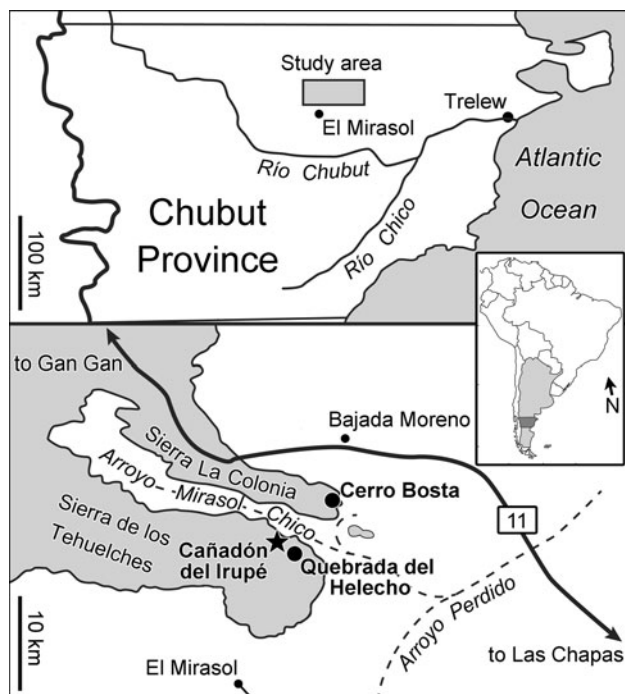


Fig. 1 Location of La Colonia fossil localities bearing marsileaceous macro- and microfossil remains. The El Uruguayo fossil vertebrate locality is near the position of Quebrada del Helecho (fig. 1 in Rougier et al. 2009). Map modified from fig. 1 in Rougier et al. (2009) and fig. 1 in Cúneo et al. (2013)

South American material from *Marsileaceaphyllum* and restricts *Marsileaceaphyllum* to vegetative material consisting of or attached to leaves with architecture most resembling that of *Marsilea* among extant marsileaceous genera.

Systematic Paleontology

The fossils documented in this paper are from the Late Cretaceous (Campanian–Maastrichtian) part of the La Colonia Formation, Chubut Province, Argentina. The La Colonia Formation consists of three superposed facies associations, the middle of which is thought to be Campanian to Maastrichtian in age and is interpreted as representing a coastal habitat with freshwater influences (Ardolino and Delpino 1987; Pascual et al. 2000). The climate under which the sediments of this facies association were deposited is interpreted as having had dry and wet seasons (Ardolino and Delpino 1987), which can be inferred on the basis of distinctive sediments, sedimentary structures, presence or absence of evaporites, and fossil assemblages (Pascual et al. 2000). The wet season sediments are known to yield plant remains and a diverse vertebrate fauna, including fish, turtles, lizards, snakes, plesiosaurs, crocodiles, dinosaurs, birds, and mammals

(Bonaparte 1985; Albino 2000; Gasparini and De la Fuente 2000; Pascual et al. 2000; Gasparini et al. 2001; Kielan-Jaworowska et al. 2007; Rougier et al. 2009; Lawver et al. 2011; Sterli and De la Fuente 2011; O’Gorman et al. 2012; O’Gorman and Gasparini 2013). Sediments yielding vertebrate remains are minimally several meters higher in the formation than those yielding plant macrofossils (Fig. 1 in Pascual et al. 2000).

The known flora of the La Colonia Formation is based on reports from three localities: Cerro Bosta (Cerro Buitre in A. Archangelsky et al. 1999), Quebrada del Helecho, and Cañadón del Irupé. Remains of salvinian ferns have been found near Cerro Bosta (Fig. 1), a vertebrate locality from which turtles and elasmosaurid and polycotyloid plesiosaurs have been reported (Gasparini and De la Fuente 2000; Gasparini et al. 2001; O’Gorman and Gasparini 2013). Plant fossils include salvinian megaspores and microspore massulae with multibarbed glochidia assigned to *Paleoazolla patagonica* A. Archangelsky & al. (A. Archangelsky et al. 1999), as well as impressions of the marsileaceous fern *Regnellidium thomas-taylorii* Cúneo & al. with associated dispersed mega- and microspores assigned to the species *Molaspora lobata* (Dijkstra) Hall and *Crybelosporites* cf. *pannuceus* (Brenner) Srivastava, respectively (Cúneo et al. 2013). Two more plant macrofossil localities, Cañadón del Irupé and Quebrada del Helecho (Fig. 1), are in the geographic vicinity of the El Uruguayo fossil vertebrate locality, from which have come an enanthiornithine bird fossil (Lawver et al. 2011) and a species of mesungulid mammal (Rougier et al. 2009). *Regnellidium thomas-taylorii* macrofossils were also recovered from Quebrada del Helecho (Cúneo et al. 2013). Cañadón del Irupé is the most diverse of the known La Colonia Formation plant fossil localities, yielding aquatic angiosperms, including impressions of *Nelumbo puertae* Gandolfo & Cúneo leaves, unnamed nelumbonaceous fruit-receptacles and fruits, araceous aquatic plants, and *Typha*-like leaves; terrestrial dicot leaves assigned to five morphotypes; leafy conifer shoots; *Azolla*-like aquatic fern sporophytes; fern fronds with affinities to Dicksoniaceae; and the marsileaceous fossils described in this paper (Gandolfo and Cúneo 2005; Gandolfo et al. in press). The stratigraphic and sedimentological context of the Cañadón del Irupé locality was described by Gandolfo and Cúneo (2005).

The suite of marsileaceous fossils described herein was collected by N.R. Cúneo, M.A. Gandolfo, and small crews of students and technicians in 2003 and 2006 from the Cañadón del Irupé locality. Macrofossil specimens were prepared by staff of the Museo Paleontológico Egidio Feruglio (MEF), as necessary. Fossil spores were macerated from the macrofossil-bearing rock matrix using the methods detailed by Cúneo et al. (2013); 25 µm sieves were used to separate out microspores, and 100 µm sieves

for megaspores. Spores were mounted on stubs for examination with a scanning electron microscope (SEM). Fossil specimens are housed in the MEF (Trelew, Chubut Province, Argentina) paleobotanical collection (MPEF-Pb) and microfossil collection (MPEF-MEB). Herbarium specimens of extant ferns figured for comparative purposes are from the collections of the L.H. Bailey Hortorium Herbarium (BH, Cornell University, Ithaca, New York, USA). Anatomical slides of extant *Marsilea* sporocarps are from the Cornell University Plant Anatomy Collection (CUPAC, Department of Plant Biology, Cornell University, Ithaca, New York, USA).

Terminology and characteristics used to describe the morphology and venation of the leaflets were taken or adapted primarily from Nagalingum (2007) and Ellis et al. (2009), as most appropriate. For features in Ellis et al. (2009) that require reference to a midvein, an imaginary median longitudinal line bisecting the leaflet from petiole to apex was used in lieu of a midvein. Sporocarp anatomy was interpreted with reference primarily to Bilderback (1978) and Nagalingum et al. (2006); terms for cells, tissues, and structures were chosen from either resource according to our preferences. Terminology used to describe the megaspores is the same as that used in Cúneo et al. (2013). The term acrolamella is used throughout this text to refer only to the “solid acrolamella” sensu Schneider and Pryer (2002) found on marsileaceous spores. Order- and family-level taxonomy follows Smith et al. (2006), but Hydropteridaceae are also recognized as a family of extinct plants within Salviniales after Rothwell and Stockey (1994). Authors of supergeneric names for extant groups follow Reveal (Reveal 2009–2012). Batten and Kovach (1990) served as a resource for locating pre-1990 megaspore taxon occurrence references and synonyms.

Macrophotographs and photomicrographs of fossil and herbarium specimens were taken with a variety of digital cameras and microscopes available at the MEF and at Cornell University. Spores were photographed using a JEOL LSM-6460 SEM (Aluar S.A., Puerto Madryn, Chubut Province, Argentina). Macro- and microfossils were measured from photographs of specimens using Adobe® Photoshop® CS4 Extended Ver. 11.0 (©1990–2008 Adobe Systems Inc.). Photoshop® was also used to construct figures. In order to facilitate comparison of images across studies, some labels used on figures of anatomical slides of the sporocarps of extant *Marsilea* follow those used in Nagalingum et al. (2006).

Systematic Paleontology

Class Polypodiopsida Cronquist, Takht. & Zimmerm.

Order Salviniales Link

Family Marsileaceae Mirb.

Diagnosis of marsileaceous vegetative organs. Rhizomes bearing roots and simple, unbranched filiform or compound leaves, or isolated compound leaves. Compound leaves petiolate with two or four leaflets (sometimes more) borne oppositely or in a pseudowhorl at the petiole apex. Leaflet venation of a single order, dichotomous with anastomoses, midvein absent; frequency of anastomoses variable (venation ranging from nearly lacking anastomoses to being fully reticulate). Areoles elongate lengthwise (but may become shorter distally) and generally fusiform in shape, lacking freely-ending veinlets.

References consulted for diagnosis. Gupta (1962), Pray (1962), Gaudet (1964), Johnson (1986), Rich et al. (2001), Skog and Dilcher (1992), Kramer (1990), Nagalingum (2007), Herman and Kvaček (2010), Cúneo et al. (2013).

Genus *Marsileaceaeaphyllum* Nagalingum emend. Hermsen, Gandolfo & Cúneo

Emended generic diagnosis. Rhizomes bearing compound leaves and roots, or detached compound leaves. Leaves with four leaflets. Leaflets sessile, obovate to obdeltoid, base shape cuneate to convex, apex obtuse and rounded. Margin entire or apical portion crenate. Leaflet venation dichotomizing with few anastomoses to reticulate. Marginal vein present.

References consulted for diagnosis. Rich et al. (2001), Skog and Dilcher (1992), Nagalingum (2007), Herman and Kvaček (2010).

Type species. *Marsileaceaeaphyllum johnhallii* (J. Skog & Dilcher) Nagalingum

Species *Marsileaceaeaphyllum johnhallii* (J. Skog & Dilcher) Nagalingum, Plant Syst Evol 264: 45. 2007.

Marsilea johnhallii J. Skog & Dilcher, Am J Bot 79: 983, figs. 1–10, 11 (drawing). 1992. Basionym.

Marsilea johnhallii J. Skog & Dilcher, Skog and Dilcher, Rev Palaeobot Palynol 80: 11, pl. V, figs. 20–22. 1994.

Species diagnosis and description. Skog and Dilcher (1992): 983.

Occurrence. Near Hoisington, Cenomanian, Dakota Formation, Barton County, Kansas, USA (Skog and Dilcher 1992).

Species *Marsileaceaeaphyllum campanicum* J. Kvaček & Herman in Herman and Kvaček, Late Cretaceous Grünbach flora of Austria (Naturhistorisches Museum Wien, Vienna, Austria): 39–40, text-fig. 17 (drawing), pl. 8, figs. 1–7. 2010.

Marsilea sp., Kvaček and Herman, Ann Naturhistorischen Mus Wien 106A: fig. 1b (drawing). 2004.

Marsilea campanica J. Kvaček & Herman, nom. nud., in Herman and Kvaček, Acta Palaeobot: fig. 2H (drawing). 2007.

Species diagnosis and description. Herman and Kvaček (2010): 39–40.

Occurrence. Grünbach am Schneeberg, Campanian, Grünbach Formation, Lower Austria, Austria (Herman and Kvaček 2010).

Species *Marsileaceaphyllum* cf. *campanicum*

Marsilea sp., Rich et al., PALAIOS 16: 610–611, figs. 3, 4B, 4D. 2001.

Marsileaceaphyllum sp. A, Nagalingum, Plant Syst Evol 264: 48. 2007.

Description of material. Rich et al. (2001): 610–611.

Occurrence. Dry Creek Environmental Education Area (Bureau of Land Management, United States Department of the Interior), Eocene, Wasatch Formation, Johnson County, Wyoming, USA (Rich et al. 2001).

Genus *Mirasolita* Hermsen, Gandolfo & Cúneo, gen. nov.

Generic diagnosis. Compound leaves with two leaflets. Each leaflet with a petiolule and reniform lamina. Leaflet base shape cordate, apex obtuse and rounded. Margin entire. Leaflet venation reticulate.

Type species here designated. *Mirasolita irupensis* Hermsen, Gandolfo & Cúneo, sp. nov.

Etymology. The generic name refers to the Arroyo Mirasol Chico, a creek in the vicinity of the type locality.

Species *Mirasolita irupensis* Hermsen, Gandolfo & Cúneo, sp. nov. (Fig. 2a–d)

Holotype here designated. MPEF-Pb 5522. Fig. 2a.

Paratypes. MPEF-Pb 869, 5520 (Fig. 2b), 5521 (Fig. 2c), 5523–5526, 5528, 5726 (Fig. 2d).

Etymology. The specific epithet refers to the type locality of the species.

Locality. Uppermost level of the La Colonia Formation (middle facies association, Campanian–Maastrichtian) at the Cañadón del Irupé locality near Arroyo Mirasol Chico, Los Altares (4369-IV), Chubut Province, Patagonia, Argentina.

Species description. This species includes leaves with two glabrous leaflets borne oppositely at the apex of a petiole (Fig. 2a). The leaflets have a reniform lamina (Fig. 2b) 1.1 to at least 2.1 cm long and 1.7–2.2 cm wide (length-to-width ratio <1:1) and an elongate petiolule (Fig. 2a, c, d) 3.5–6.5 mm in length. The base of the each leaflet is cordate in shape (Fig. 2a–d). The apex is obtuse and rounded, and the margin is entire (Fig. 2a, b, d). The leaflets display a single order of reticulate venation with no midvein. The areoles are elongate lengthwise and frequently fusiform and polygonal in shape with up to six sides; they are more elongate toward the base of the lamina and shorter distally (Fig. 2a–d). No freely ending veinlets occur within the areoles. The marginal venation is indistinct.

Genus *Lugiomarsiglia* Gandolfo, Hermsen & Cúneo, gen. nov.

Generic diagnosis. Stalked sporocarps, elliptical to ovoid to reniform in lateral view. Point of attachment of the

stalk to the proximal sporocarp wall displaced toward the dorsal side of the sporocarp. Raphe and teeth absent, sporocarp surface glabrous. Sporocarp wall with at least one distinct layer of macrosclereids. Sporangia circular to obovate in outline.

Type species here designated. *Lugiomarsiglia aquatica* Gandolfo, Hermsen & Cúneo, sp. nov.

Etymology. *Lugiomarsiglia* refers to Luigi Marsigli (1656–1730), for whom the extant genus *Marsilea* was erected by Linnaeus (J. Reveal, pers. comm. to M.A. Gandolfo, 2012).

Species *Lugiomarsiglia aquatica* Gandolfo, Hermsen & Cúneo, sp. nov. (Fig. 3a–f)

Holotype here designated. MPEF-Pb 5527, Fig. 3a, d–f. Paratypes. MPEF-Pb 909, 5529–5534. Fig. 3a–c.

Etymology. The specific epithet refers to the aquatic habit of these plants.

Locality. Uppermost level of the La Colonia Formation (middle facies association, Campanian–Maastrichtian) at the Cañadón del Irupé locality near Arroyo Mirasol Chico, Los Altares (4369-IV), Chubut Province, Patagonia, Argentina.

Species description. This species includes sporocarps preserved as compressions. The sporocarps are elliptical to ovoid to reniform in lateral view (Fig. 3a–d), 2.5–7.5 mm long, and 1.5–5.5 mm high (length-to-height ratio 1.4:1–2.2:1). They are glabrous and lack teeth and a raphe (Fig. 3a–d). Each sporocarp is attached to the end of a stalk (Fig. 3a, b, d) more than 2.5 mm in length (stalks only partially preserved) and between 0.5 and 1.5 mm in width. The point of attachment of the stalk is displaced toward the dorsal side of the sporocarp (Fig. 3a, b, d). The sporocarp wall is up to 0.5 mm thick and sclerenchymatous, with at least one distinct layer of elongate structures interpreted as macrosclereids (Fig. 3e–f). Evidence of sorophore delimitation is ambiguous. The number and exact arrangement of the sori are ambiguous. The sporangia are circular to obovate in shape and of variable size, ranging to slightly over 1.0 mm in diameter.

Genus *Molaspora* Schemel emend. Hall

Species *Molaspora lobata* (Dijkstra) Hall (Fig. 4a, b)

Material examined. MPEF-MEB 5503, 5504.

Locality. Uppermost level of the La Colonia Formation (middle facies association, Campanian–Maastrichtian) at the Cañadón del Irupé locality near Arroyo Mirasol Chico, Los Altares (4369-IV), Chubut Province, Patagonia, Argentina.

Description, Cañadón del Irupé material only. Dispersed megaspores with a nearly spheroidal body (Fig. 4a), 342–360 µm along the polar axis and 319–362 µm wide along the widest portion of the equatorial diameter (length-to-width ratio 0.99:1–1.07:1). An acrolamella 37 µm in height and 128 µm in width is present on the proximal pole (Fig. 4a). The sculpture of the spore body is baculate, with baculae of uniform size (Fig. 4b).

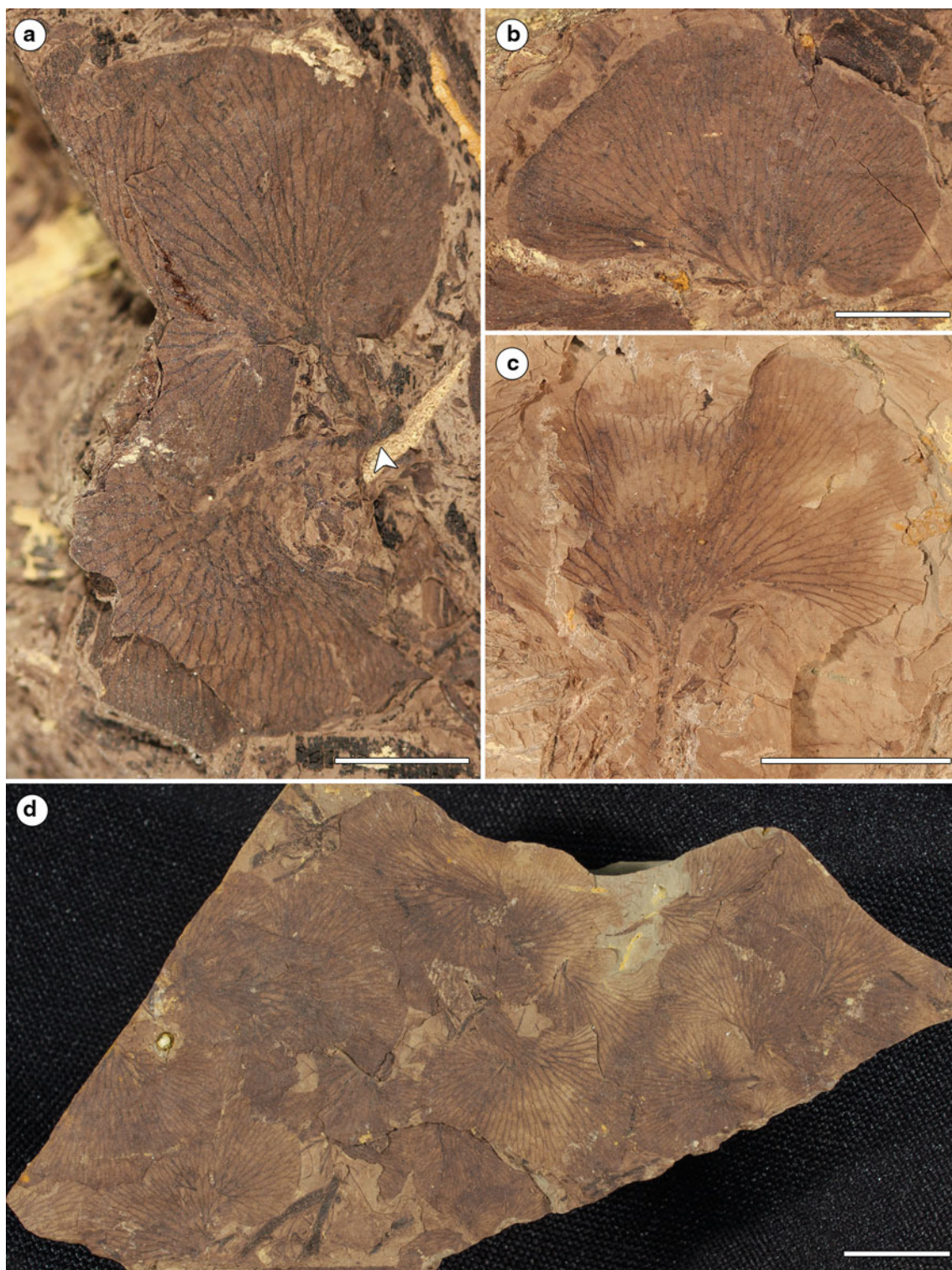


Fig. 2 *Mirasolita irupensis* Hermsen, Gandolfo & Cúneo, sp. nov. **a** Two leaflets attached via petiolules to the apex of a common petiole; arrowhead indicates point of attachment of petiolules to apex of petiole. Holotype, MPEF-Pb 5522. **b** Lamina of single leaflet showing reniform shape and reticulate venation pattern.

MPEF-Pb 5520. **c** Single leaflet showing reticulate venation pattern and elongate petiolule. MPEF-Pb 5521. **d** Specimen showing multiple leaflets with characteristic reniform laminae, elongate petiolules, and reticulate venation. MPEF-Pb 5726. *Scale bars a–c* 5 mm; *d* 10 mm

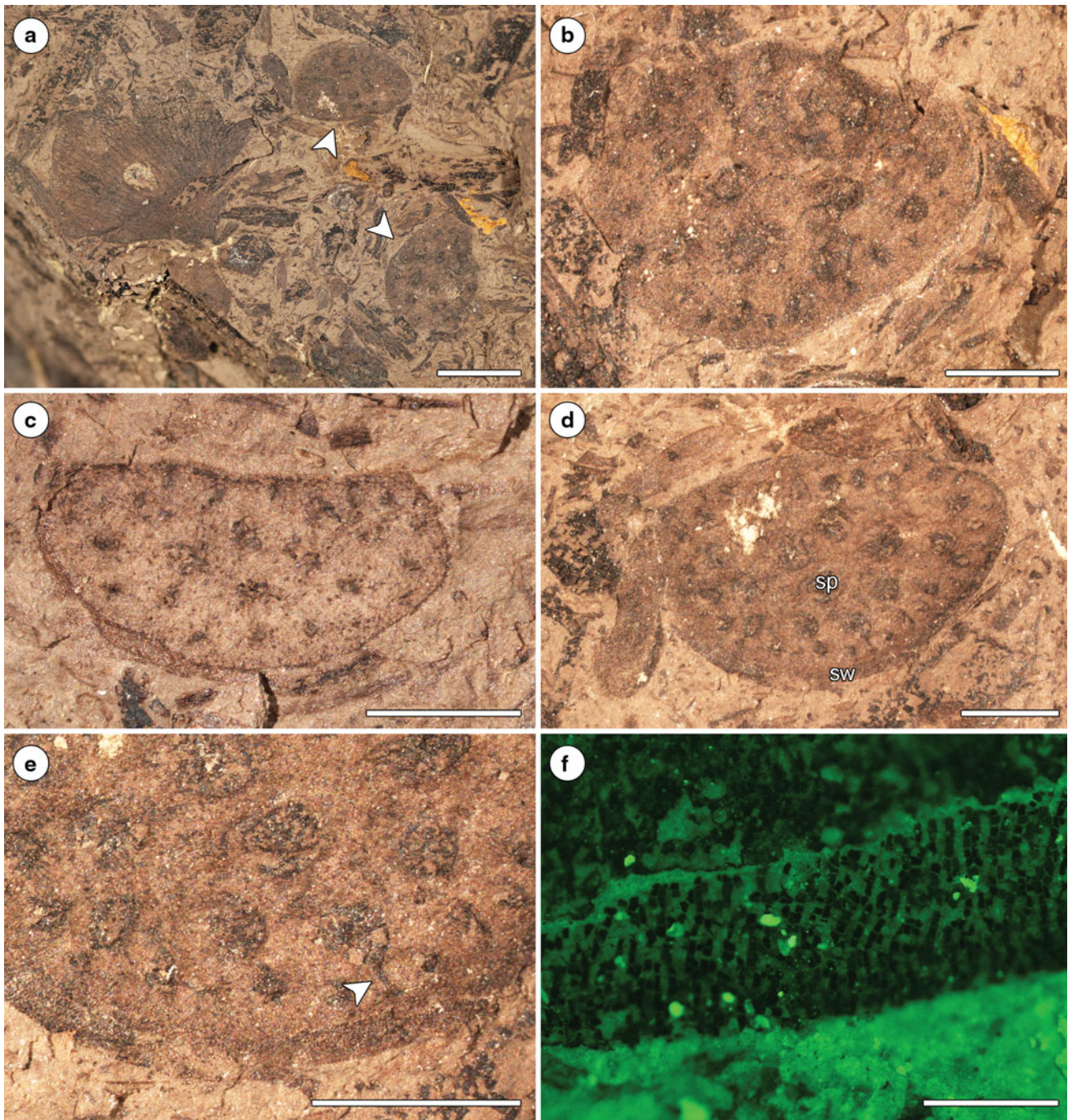


Fig. 3 *Lugiomarsiglia aquatica* Gandolfo, Hermsen & Cúneo, sp. nov. **a** Sporocarps (arrowheads) in close proximity to *Mirasolita* leaflet. Holotype and paratypes, MPEF-Pb 5527. **b** Ovoid sporocarp with stalk. MPEF-Pb 5527. **c** Nearly reniform sporocarp. MPEF-Pb 5530. **d** Elliptical sporocarp with flatter dorsal side and attached stalk, clearly

showing sclerenchymatous sporocarp wall (sw) and sporangia (sp). Holotype, MPEF-Pb 5527. **e** Details of possibly stalked sporangium (arrowhead) and adjacent sporocarp wall. Holotype, MPEF-Pb 5527. **f** Detail of sclerenchymatous sporocarp wall under epifluorescence. Holotype, MPEF-Pb 5527. Scale bars **a** 5 mm; **b–e** 2 mm; **f** 0.1 mm

Discussion

Emendation of *Marsileaceaephyllum*

In order to address the weaknesses of the original *Marsileaceaephyllum* concept, we have provided an informal

diagnosis for vegetative organs of Marsileaceae as well as an emended diagnosis for *Marsileaceaephyllum*. The informal diagnosis for fossil vegetative organs assignable to the family expands upon features outlined in the original diagnosis for *Marsileaceaephyllum*, which was intended by Nagalingum (2007) to encompass all fossil vegetative

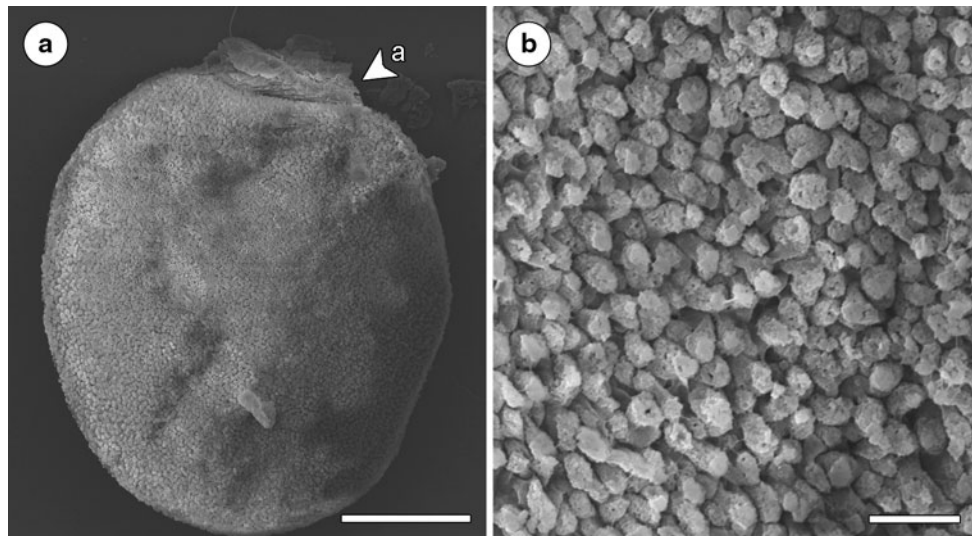


Fig. 4 *Molasporea lobata* megaspores macerated from the Cañadón del Irupé sediments. **a** Equatorial view showing baculate surface sculpture and acrolamella (a). MPEF-MEB 5503. **b** Detail of surface

sculpture showing baculae of uniform size. MPEF-MEB 5504. Scale bars **a** 100 μm ; **b** 10 μm

organs of Marsileaceae lacking attachment to reproductive structures. As identified by Nagalingum (2007: 44), diagnostic features for marsileaceous vegetative remains include leaflets that have dichotomizing venation and vein anastomoses forming polygonal areoles that are elongate and fusiform, while also lacking a midvein. Since Nagalingum's (2007) diagnosis also encompasses the venation pattern of the leaflets of the pinnately compound leaves of *Hydropteris pinnata* (Hydropteridaceae: Rothwell and Stockey 1994), we have added whole-leaf architecture to the diagnosis of marsileaceous vegetative material. We have also explicitly specified that marsileaceous leaflets lack freely ending veinlets in their areoles, a distinguishing characteristic mentioned by Nagalingum (2007: 45) in her discussion, but not her formal diagnosis of the fossil genus.

In addition to its distinctive leaf architecture, each of the living genera of Marsileaceae has its own highly distinctive megaspore morphology (Tryon and Tryon 1982; Schneider and Pryer 2002). Current evidence from the fossil record favors the hypothesis that *Regnellidium*-like megaspores with baculate sculpture where the baculae are all roughly the same size are plesiomorphic among the megaspore morphologies of extant Marsileaceae (Lupia et al. 2000; Cúneo et al. 2013). When dispersed, this megaspore type is assigned to the taxon *Molasporea lobata* (Batten 1988; Lupia et al. 2000; Batten et al. 2011). The evidence that the *M. lobata* megaspore type may be plesiomorphic for the entire extant family consists of three major components: (1) *Molasporea lobata*-type spores occur in situ and associated with marsileaceous macrofossils of a variety of morphologies in Cretaceous sediments (discussed below); (2) the first appearance of *M. lobata* spores in the Albian to

Cenomanian (documented by, e.g., Douglas 1973; Sweet 1979; Kovach and Dilcher 1988; Tosolini et al. 2002, 2012; Batten et al. 2010) predates by a significant duration the first appearance of *Marsilea*-like (Oligocene: Dorofeev 1963, 1981), *Pilularia*-like (Miocene: Dorofeev and Velichkevich 1971; Dorofeev 1981), and definitive *Regnellidium* (Eocene: Dorofeev 1981; Batten et al. 2011) megaspores in the Cenozoic (see also Nagalingum 2007; Cúneo et al. 2013); and (3) of species of *Arcellites* and *Molasporea*—the two fossil form genera thought to represent marsileaceous megaspores in the Cretaceous (Collinson 1991, 1996)—*M. lobata* comes nearest temporally to the first reports of megaspores assigned to the extant genera and is last recorded in the Paleocene to Eocene (Dijkstra 1959; Kovach and Batten 1989; see Batten and Collinson 2001 for updated age information). We agree with Collinson (1996) that if fossil *Marsilea* is defined in part by its distinct megaspore morphology—as we here concur that it should be—then Cretaceous fossils with sporophyte morphology consistent with *Marsilea* that are thought to have produced non-*Marsilea*-type megaspores should be recognized as taxonomically separate from the extant genus.

We have provided a revised circumscription for *Marsileaceaeaphyllum* that includes only those fossils that have leaves with four obovate to obdeltoid leaflets, similar to leaves of extant *Marsilea* (Fig. 5a, b), but for which sporocarp and spore structure is unknown or ambiguous. *Marsileaceaeaphyllum* in its current incarnation should thus be interpreted as a taxon for fossils with leaf form similar to extant *Marsilea* but whose exact relationship to one another and to the modern genera of Marsileaceae is not well understood due to insufficient supplementary data

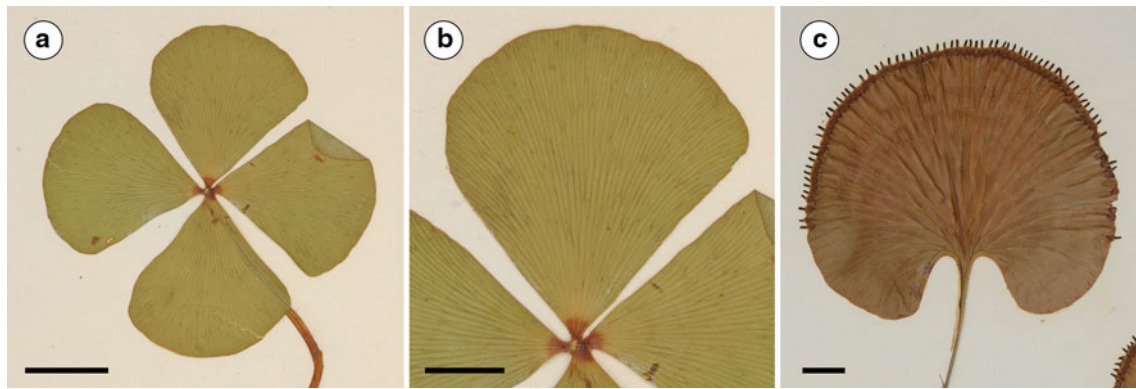


Fig. 5 Examples of extant fern leaves. **a** *Marsilea quadrifolia* L. leaf with four obovate leaflets. BH 000 048 569 (Massachusetts, USA: George Golding Kennedy *s.n.*). **b** Detail of a leaflet from the same leaf showing reticulate venation pattern. **c** *Cardiomanes reniforme* (G. Forst.) C. Presl. leaf that is similar in shape to *Mirasolita* leaflets. BH 000 053 972 (New Zealand: *s.n.*, ex Herbarium of S.H. Burnham). Scale bars **a**, **c** 1 cm; **b** 5 mm

Table 1 Comparative leaf and megaspore morphology of living and extinct genera of Marsileaceae

Genus	No. of leaflets	Leaflet attachment	Leaflet base shape	Leaflet vein anastomoses	Marginal vein	Megaspore
<i>Marsilea</i>	4	Sessile to very short-petiolate	Concave, cuneate, or convex	Frequent, venation reticulate	Discontinuous, indistinct, irregular course	<i>Marsilea</i> type
<i>Marsileaceaphyllum</i>	4	Sessile	Cuneate to convex	Variable	<i>Regnellidium</i> -like or <i>Marsilea</i> -like	Unknown (<i>Molaspora</i> or <i>Arcellites</i> in the Cretaceous?)
<i>Mirasolita</i>	2	Long-petiolate	Cordate	Frequent, venation reticulate	Probably <i>Marsilea</i> -like	Probably <i>Molaspora lobata</i>
<i>Pilularia</i>	0	–	–	–	–	<i>Pilularia</i> type
<i>Regnellidium</i>	2	Sessile	Subtruncate to truncate, concavo-convex to slightly cordate	Infrequent	Continuous, distinct, smooth course	<i>Regnellidium</i> type, incl. <i>Molaspora lobata</i>
<i>Regnellites</i>	2	Sessile	Truncate	Infrequent	Absent	Unknown

Note that *Marsilea* and *Regnellidium* exhibit heterophylly—or different submerged, floating, and terrestrial leaf morphologies (Johnson 1986)—and the following characteristics refer to the floating and terrestrial forms. Sources of information: Pray (1962), Gaudet (1964), Johnson (1986), Kovach and Dilcher (1988), Skog and Dilcher (1992), Rich et al. (2001), Alonso Paz and Bassagoda (2002), Schneider and Pryer (2002), Yamada and Kato (2002), Nagalingum (2007), Herman and Kvaček (2010), and Cúneo et al. (2013)

from reproductive structures. This is in the spirit of, although narrower than, Nagalingum’s (2007) original concept of the genus. If, for example, the *Marsileaceaphyllum* leaves from the Eocene Wasatch Formation of Wyoming, which are morphologically nearly identical to *Marsilea* leaves (Rich et al. 2001), were to be found in association with *Marsilea*-like megaspores, transfer to *Marsilea* might be justified on circumstantial grounds. The morphological differences among leaves of the modern genera of Marsileaceae and the fossil genera presented in this paper are summarized in Table 1.

We recognize only two species and an additional occurrence of *Marsileaceaphyllum*, down from four species and three morphotypes recognized by various authors

from 2007 to 2010 (Nagalingum 2007; Hu et al. 2008; Herman and Kvaček 2010). The venation and morphology of the leaflets varies slightly among the three occurrences of *Marsileaceaphyllum*, with the Cenomanian type species (Skog and Dilcher 1992) being distinct from the younger Campanian Grünbach (Herman and Kvaček 2010) and middle Eocene Wasatch (Rich et al. 2001) material. The type, *Marsileaceaphyllum johnhallii*, has leaflets with a margin that is typically crenate rather than entire apically and leaflet venation that apparently has more anastomoses (Skog and Dilcher 1992). Presence or absence of teeth or lobes on the apical portion of the leaflet is a character that varies intraspecifically in Marsileaceae, however, and is determined by the environmental conditions under which

the leaves formed (Gupta 1962; Johnson 1986). Images of *M. johnhallii* (figs. 5–7 in Skog and Dilcher 1992) also suggest that leaflets of the taxon have a distinct and continuous marginal vein similar to that found in *Regnellidium* leaflets (see Pray 1962). As described by Herman and Kvaček (2010), the marginal vein of *Marsileaceaphyllum campanicum* is different in apparently being like that of living *Marsilea*, in which the marginal vein is less distinct, has a slightly irregular course, and is sometimes discontinuous (Gaudet 1964). The marginal venation of the Watsch material was not described.

Herman and Kvaček (2010) identified the *Marsileaceaphyllum campanicum* specimens from the Grünbach flora as the same material first alluded to as *Marsilea* in a report by Krasser (1906) and later under the nomen nudum “*Marsilea Nathorsti*” by Seward (1910, citing personal communication from Krasser). In neither of these early publications were specimens described or illustrated, however, and a description and photographs of the Grünbach fossils were not published until 2010 (plate 8, figs. 1–7 in Herman and Kvaček 2010). Skog and Dilcher (1992) and Rich et al. (2001) listed “*Marsilea nathorsti*” in tables of *Marsilea*-like fossils, and identified the species as possibly representing fossil leaves. The *Marsileaceaphyllum* material from the Eocene of North America informally described by Rich et al. (2001) closely matches the description of *M. campanicum* leaves by Herman and Kvaček (2010), both in qualitative details and the overall dimensions of the leaflets. We have refrained from definitively transferring the Eocene leaves to *M. campanicum* here because we have not examined the original specimens of either the North American or European material.

Four other taxa have been assigned to *Marsileaceaphyllum* in the past. *Marsileaceaphyllum* sp. B of Nagalingum (2007) from the Albian Citadel Bastion locality, Neptune Glacier Formation, Alexander Island, Antarctica; *Marsileaceaphyllum* sp. C of Nagalingum (2007) from the Cenomanian Devils Kitchen locality, Eumeralla Formation, Victoria, Australia (see Tosolini et al. 2012 for revised age); *Marsileaceaphyllum lobatum* Nagalingum from the Albian Citadel Bastion and North Coal Nunatak localities of the Neptune Glacier Formation, Alexander Island, Antarctica (Nagalingum 2007); and *Marsileaceaphyllum mahisensis* Hu & al. from the Albian Mahis locality, Jarash Formation, Jordan (Hu et al. 2008).

Of these, “*Marsileaceaphyllum*” sp. B is an informal taxon based on a single leaf or leaflet apex exhibiting dichotomizing venation with anastomoses and a marginal vein (Nagalingum 2007). This specimen is consistent with leaflets of Marsileaceae in its venation pattern, but it is very incomplete. “*Marsileaceaphyllum*” sp. C is represented by two leaves. This leaf type has four petiolulate, obovate leaflets lacking venation but with an indumentum of

trichomes (Nagalingum 2007). Given that the leaflets of “*Marsileaceaphyllum*” sp. C appear whorled (Nagalingum 2007) and that the specimens occur in the same locality as marsileaceous spores assigned to several species of *Arcellites* as well as *Molaspora lobata* (Tosolini et al. 2002, 2012), their assignment to Marsileaceae is plausible. Despite this, neither “*Marsileaceaphyllum*” sp. B nor C falls within the revised diagnosis of *Marsileaceaphyllum*. We recommend treating these morphotypes as cf. Marsileaceae sp.

“*Marsileaceaphyllum*” *lobatum* is based on four leaves or detached leaflets with variously lobed margins, reticulate venation, and no marginal vein (Nagalingum 2007). Lack of a marginal vein and ignorance of the full leaf architecture places the leaflets outside of the revised diagnosis of *Marsileaceaphyllum*. “*Marsileaceaphyllum*” *mahisensis* is based on structures interpreted by Hu et al. (2008) as detached leaflets; they have an obovate shape and lack a petiole, similar to the leaflets of *Marsileaceaphyllum*. The venation of the fossil leaflets differs from that of leaflets of Marsileaceae in that the Mahis laminas are bisected by a weak midvein (figs. 2C–I, 3A–E in Hu et al. 2008). Hu et al. (2008) tested the phylogenetic position of “*Marsileaceaphyllum*” *mahisensis* using a morphological matrix modified from Pryer (1999); the results of that analysis suggest that “*Marsileaceaphyllum*” *mahisensis* is nested within the extant *Marsilea* clade. It should be noted, however, that the analysis apparently included only the terminals representing extant Salviniales from the Pryer (1999) matrix, excluding fern taxa outside of the order and the extinct salvinian taxon *Hydropteris pinnata*. This all but insured that “*Marsileaceaphyllum*” *mahisensis* would be resolved within Marsileaceae, and with *Marsilea* in particular. Because the full leaf architecture of these structures cannot be confirmed and because their systematic affinities have not been fully explored, we consider their relationship to Marsileaceae equivocal and recommend that they not be included in *Marsileaceaphyllum* unless specimens preserving more definitive diagnostic information are obtained.

There are two other reports of leaves assigned to or considered to have affinities to *Marsilea*, which are thus possible candidates for transfer to *Marsileaceaphyllum*. The first of these, from the Albian Pur-River Section of the Bhuj Formation, Gujarat, India (Banerji 1987; see Rai 2006 for age), is poorly documented (see also Nagalingum 2007). The second, from the Oligocene Margargaria River locality of the Chilga beds, Amara, Ethiopia, includes leaves with up to four leaflets in a whorl (García Massini et al. 2010) that are similar in overall morphology to “*Marsileaceaphyllum*” sp. C of Nagalingum (2007) (compare Fig. 3a, b, and d in Nagalingum 2007 to Fig. 8.7 in García Massini et al. 2010). As in extant *Marsilea* (see Nagalingum 2007), the venation of the Margargaria River leaflets is reticulate, there are no freely

ending veinlets, a midvein is absent, a marginal vein is present, and the areoles are elongate lengthwise (figs. 8.5, 8.8 in García Massini et al. 2010). In contrast to the leaflet venation of other members of Marsileaceae, however, the areoles of the Margargaria River leaflets are not fusiform but distinctly rectangular or nearly so (compare Figs. 8.5, 8.8 in García Massini et al. 2010 to Figs. 2a–d and 5b in this paper and Fig. 6 in Gaudet 1964). To date, no co-occurring marsileaceous sporocarps or spores have been described from the Chilga beds. We consider the assignment of the Ethiopian material uncertain pending more detailed comparison of its structure with that of leaves of extant *Marsilea* and to species of *Marsileaceaphyllum*.

Comparative morphology of *Mirasolita*

The Cañadón del Irupé leaflets are consistent with the leaflets of Marsileaceae (see Nagalingum 2007 for characters of the leaflets of Marsileaceae) in the following features: they lack midveins, have a dichotomizing and anastomosing venation pattern, and have areoles that are elongate lengthwise, often fusiform, and lack freely ending veinlets (compare Figs. 2a–d, 5a, b). Also, the complete leaves consist of leaflets attached to the apex of a petiole (Fig. 2a), as in extant *Marsilea* and *Regnellidium* (Fig. 5a; Tryon and Tryon 1982; Kramer 1990).

One specimen of *Mirasolita* shows two leaflets attached to a petiole (Fig. 2a). Given the width of the reniform distal ends of the leaflets—wherein more than two leaflets probably could not occur in a single pseudowhorl without overlapping—and the lack of clear evidence for additional leaflets, we interpret this as representing a complete leaf. The leaflets have distinct, elongate petiolules (Fig. 2a, c, d). This is a feature not observed in extant Marsileaceae (Nagalingum 2007), although *Marsilea* leaflets can sometimes appear very short petiolulate (fig. 6, 7 in Gaudet 1964). In shape, *Mirasolita* leaflets are convergent with leaves of several extant leptosporangiate fern species (e.g., *Adiantum reniforme* L., *Cardiomanes reniforme* (G. Forst.) C. Presl, and *Lindsaea reniformis* Dryand.) that are petiolate with reniform laminae lacking a midvein (compare Figs. 2b–d and 5c; see also Wagner 1952). *Mirasolita* leaflets have a reticulate venation pattern consistent with that of extant *Marsilea* (compare Figs. 2a–d, 5b). The marginal venation is difficult to observe but is likely similar to that reported by Gaudet (1964) for *Marsilea*, in which most but not all of the anastomoses close at or near the apical margin of the leaf, resulting in a marginal vein that has a discontinuous, slightly irregular course. *Mirasolita* leaflets are glabrous and their margins are entire (Fig. 2a, b, d); in extant *Marsilea*, these features are ecophenotypic and more characteristic of floating than of terrestrial leaves (Gupta 1962; Johnson 1986).

Despite the similarities in venation pattern, *Mirasolita* differs from *Marsilea* in having two leaflets per leaf rather than four and in having leaflets with relatively long petiolules and cordate bases (Table 1). These are also features that distinguish it from the newly emended *Marsileaceaphyllum* (Table 1). Fossil leaves from the Cenomanian of Australia (“*Marsileaceaphyllum*” sp. C of Nagalingum 2007; see Tosolini et al. 2012 for revised age) have leaflets that are somewhat similar to those of *Mirasolita*, in that each has a distinct petiolule (Nagalingum 2007). These leaves differ, however, in having four leaflets and laminar trichomes (fig. 3a–d in Nagalingum 2007), although the latter is an ecophenotypic characteristic in extant Marsileaceae (Johnson 1986). The leaflet venation of “*Marsileaceaphyllum*” sp. C is unknown (Nagalingum 2007).

Leaf and leaflet macrofossils attributed to Marsileaceae have now been identified at three localities in the La Colonia Formation: Cañadón del Irupé, Cerro Bosta, and Quebrada del Helecho (Fig. 1). The species from Cerro Bosta and Quebrada del Helecho was described by Cúneo et al. (2013) as *Regnellidium thomas-taylorii* on the basis of numerous specimens of leaves and associated rhizomes bearing roots. Although both kinds of leaves have two leaflets and clearly represent Marsileaceae, *Mirasolita irupensis* and *R. thomas-taylorii* are quite distinct from one another in several respects. The leaflets of *Mirasolita* have a cordate base and a petiolule (Fig. 2a, c, d), whereas those of *R. thomas-taylorii* have a concavo-convex base with no elongate petiolule (figs. 2B, D in Cúneo et al. 2013). Further, leaflets of *M. irupensis* have a reticulate venation pattern and lack a strong and continuous marginal vein (Fig. 2a–d), whereas those of *R. thomas-taylorii* have dichotomous venation with rare anastomoses and a prominent and continuous marginal vein (Cúneo et al. 2013), as is also characteristic of the living species *Regnellidium diphyllum* (Pray 1962).

Comparative morphology of *Lugiomarsiglia*

The sporocarp (Fig. 6a–d) is a spore-bearing structure that is homologous across and synapomorphic for the order Salviniales. It consists of homosporangiate (Salvianaceae) or heterosporangiate (Marsileaceae) sori that are borne on a sorophore that is completely enclosed within a sorophore envelope (hypothesized to be secondarily lost in *Salvinia*), the defining characteristic of the sporocarp (Nagalingum et al. 2006). In Marsileaceae, the sorophore envelope is robust and sclerenchymatous and is typically called a “sporocarp wall,” a characteristic unique to sporocarps of plants within the family (Fig. 6a, b; Bilderback 1978; Nagalingum et al. 2006). The sporocarp wall of Marsileaceae is relatively complex and consists of a uniseriate epidermis underlain by macrosclereids, underneath which

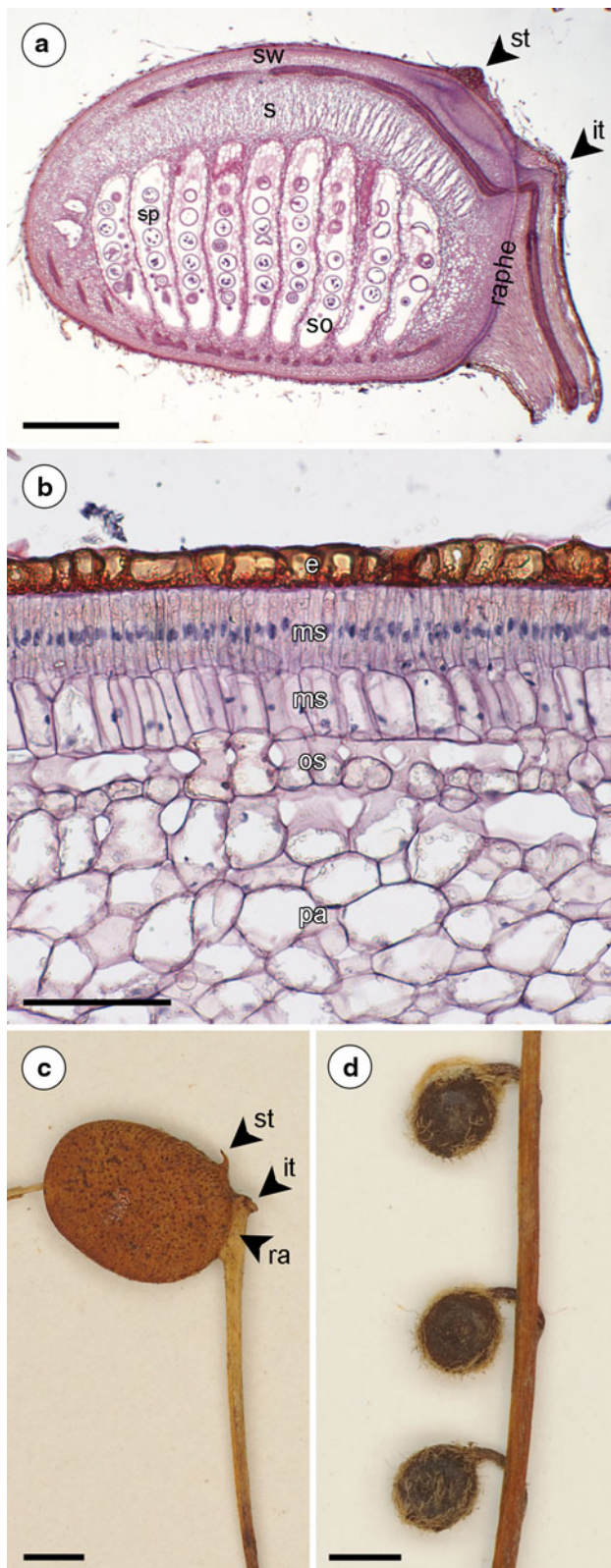


Fig. 6 Sporocarps of extant *Marsilea*. **a** Median longitudinal section of sporocarp of *M. quadrifolia* L. showing major structural features, including the sporocarp wall (sw), the sorophore (s), the sori (so), sporangia (sp), the raphe, the inferior tooth (it), and the superior tooth (st). CUPAC 0000614. **b** Detail of layers in sporocarp wall of *M. quadrifolia* showing epidermis (e), two layers of immature macrosclereids (ms), immature osteosclereids (os), and parenchyma (pa). CUPAC 0000615. **c** *M. uncinata* A. Braun sporocarp with raphe (ra) and inferior (it) and superior (st) teeth. BH 000 048 568 (Germany, cultivated: *s.n.*, ex Herbarium of A. Braun). **d** *M. polycarpa* Hook. & Grev. sporocarps lacking a raphe or teeth. BH 000 048 570 (Bora Bora: *H. St. John* 17414). Scale bars **a** 0.5 mm; **b** 100 μ m; **c**, **d** 2 mm

macrosclereids and the parenchyma, composed of cells that have been described as “I-shaped” (Johnson 1986) or “hourglass-shaped” (Lupia et al. 2000); according to Bilderback (1978), these cells differentiate into osteosclereids when mature (Fig. 6b). The internal organization and venation pattern of the sporocarps, as well as the shape and mode of attachment of the sporangia to the receptacles, are characteristic for each of the living genera of Marsileaceae (Schneider and Pryer 2002; Nagalingum et al. 2006).

Lugiomarsiglia aquatica clearly has affinities with Salviniales because the taxon consists of reproductive structures that satisfy the definition of sporocarps. Although sori cannot be unambiguously discerned, a sorophore envelope exhibiting an anatomy consistent with that of the sclerenchymatous sporocarp wall of extant Marsileaceae clearly surrounds circular structures that are here interpreted as sporangia (Fig. 3b–e). There is a robust, well-defined layer in the wall of *Lugiomarsiglia* that likely represents sclerenchyma (Fig. 3e, f). Because this layer shows a pattern of elongate structures arranged in parallel, we interpret it as being composed of macrosclereids (compare Fig. 3f to 6b). No other cellular structure could be observed. The sporangia within *Lugiomarsiglia* sporocarps are more or less circular to slightly obovate in shape, and at least one sporangium appears to have a prominent stalk (Fig. 3e), although this could also be part of the receptacle to which the sporangia attach. Whether sporangial stalk or receptacle, the attachment of this structure to the sporocarp wall indicates that the receptacles that bore the sporangia were attached to the inside of the sporocarp wall, which is the condition found in sporocarps of *Marsilea* and *Pilularia* (Nagalingum et al. 2006). In *Regnellidium* sporocarps, by contrast, the receptacles are attached to the indusial walls of the sori that occur at right angles to the sporocarp walls (Nagalingum et al. 2006).

Some species of *Marsilea* have apomorphic external morphological features that are useful in distinguishing them from the more plesiomorphic sporocarp morphologies of *Pilularia*, *Regnellidium*, and other species of *Marsilea* (Nagalingum et al. 2007). One of these is presence of a raphe formed by the fusion of a length of the distal end of

is parenchyma (Fig. 6b; Bilderback 1978; Johnson 1986; Nagalingum et al. 2006). In *Marsilea*, there may additionally be a distinctive cell layer between the

the sporocarp stalk to wall of the sporocarp, such that the sporocarp appears to be borne laterally on the region of fusion rather than terminally on the stalk (Fig. 6a, c; Johnson 1988; Gupta 1962; Johnson 1986; Jacono and Johnson 2006; Nagalingum et al. 2007). Another characteristic is the presence of one or more sporocarp teeth, distinct projections that can occur in one or both of two positions: the inferior tooth at the tip of the stalk, and the superior tooth on the dorsal side of the sporocarp (Fig. 6a, c; Johnson 1986; Jacono and Johnson 2006; Nagalingum et al. 2007). Sporocarps of extant *Pilularia*, *Regnellidium*, and the small “Group I” clade of extant *Marsilea* (as defined by Schneider and Pryer 2002; Nagalingum et al. 2007) consistently lack both a raphe and teeth (see Fig. 6d for an example), characteristics that are plesiomorphic within the family (Nagalingum et al. 2007). The Patagonian fossil sporocarps do not appear to possess a raphe and show no evidence of teeth (Fig. 3a–d).

There are several other reports of fossil marsileaceous sporocarps from Laurasian and Gondwanan landmasses. Of these, sporangia with possible affinities to Marsileaceae from the Santonian of the Ingersoll Shale of Alabama, USA (Bingham et al. 2008), and possible *Marsilea* sporocarps from the Maastrichtian of the Marília Formation, Minas Gerais, Brazil (Senra and Silva e Silva 1998), have yet to be described in detail. The Ingersoll Shale material is figured and lacks a sporocarp wall (fig. 3I in Bingham et al. 2008). Some other marsileaceous sporocarps—including sporocarps considered comparable to those of *Marsilea* from the Albian of the Bhuj Formation in Gujarat, India (Banerji 1987; see Rai 2006 for age), sporocarps attributed to *Marsileaceaphyllum johnhallii* from the Cenomanian Dakota Formation of Kansas, USA (Skog and Dilcher 1992), and a putative sporocarp ascribed to *Regnellidium thomas-taylorii* from the La Colonia Formation of Argentina (Cúneo et al. 2013)—were attributed to Marsileaceae due primarily to the fact that they were found in association with leaves that have architecture diagnostic for or suggestive of Marsileaceae. These putative sporocarps are similar to *Lugiomarsiglia* in being stalked and lacking any indication of a raphe or teeth (text-fig. 1d and figs. 17–20 in Banerji 1987; figs. 8–10 in Skog and Dilcher 1992; Cúneo et al. 2013), but apparently show no internal structure.

Additional sporocarp material preserved as compressions was found attached to the *Regnellites nagashimae* Yamada & Kato plant from the Tithonian to Berrasian Kiyosue Formation of Honshu Island, Japan (Yamada and Kato 2002; see also Yamada and Ohno 2005 and Kawamura 2010 on stratigraphy). As described by Yamada and Kato (2002), these sporocarps are stalked, circular or elliptical in shape, and lack teeth. They tend to be slightly larger than *Lugiomarsiglia* sporocarps (minimally

8 mm × 5 mm), and differ in being erect on the stalk and in having an indumentum of conspicuous trichomes (figs. 2A–B, 3D, 6 in Yamada and Kato 2002). No evidence of a raphe was reported.

Several other fossil sporocarps are anatomically preserved and can be more thoroughly compared with sporocarps of *Lugiomarsiglia*. The first of these, *Regnellidium upatoiensis* Lupia & al., represents charcoalfied marsileaceous mesofossil sporocarps from the Santonian Eutaw Formation (or equivalent) of Georgia, USA (Lupia et al. 2000). As described by Lupia et al. (2000), these sporocarps were not found attached to stalks and are in the size range of *Lugiomarsiglia* sporocarps. They have the sclerenchymatous wall characteristic of Marsileaceae, although the wall is relatively thin at a maximum of 95 µm thick. No evidence of a raphe or teeth was reported. Lupia et al. (2000) assigned *R. upatoiensis* to *Regnellidium* among Marsileaceae based on the structure of the sporocarp wall and particularly on the morphology, sculpture, and wall structure of its in situ spores.

The best understood specimens representing sporocarps with affinities to Marsileaceae come from the Maastrichtian Mohgaonkalan flora of the Deccan Intertrappean Beds, Madhya Pradesh, India, and are assigned to the extinct genus *Rodeites* Sahni (Sahni in Sahni and Sitholey 1943; Mahabálé 1956; Chitaley and Paradkar 1971, 1972; Paradkar and Barlinge 1981; see Kumaran et al. 1997 for age). These fossils, originally described by Sahni (in Sahni and Sitholey 1943), are anatomically preserved in a siliceous matrix. *Rodeites* currently includes three species—*R. dakshini* Sahni, *R. polycarpa* Chitaley & Paradkar, and *R. intertrappeana* Paradkar & Barlinge—distinguished based on whether and how the sporocarps are grouped (Paradkar and Barlinge 1981). Like those of *Lugiomarsiglia*, sporocarps of *Rodeites* are stalked, elliptical in shape, and lack a raphe and teeth (Paradkar and Barlinge 1981); they are larger than *Lugiomarsiglia* sporocarps, with a maximum length of about 1.6 cm (Chitaley and Paradkar 1972). As in all Marsileaceae, the sporocarp wall in *Rodeites* has several distinct, concentrically arranged cell layers, including one composed of macrosclereids (“prismatic layer” of Chitaley and Paradkar 1971, 1972); the wall is somewhat thicker than that of *Lugiomarsiglia* sporocarps at 0.45–0.65 mm thick (Chitaley and Paradkar 1971, 1972). Inside each *Rodeites* sporocarp are sori with in situ mega- and microspores, the megaspores resembling those of extant *Regnellidium* and the dispersed spore taxon *Molaspora lobata* (Sahni in Sahni and Sitholey 1943; Chitaley and Paradkar 1972). The receptacles bearing the sporangia occur on the sporocarp walls rather than the indusial cross-walls within the sporocarp (Paradkar and Barlinge 1981; Nagalingam 2007), as may be the case in *Lugiomarsiglia*.

The South American fossil record of Marsileaceae and the significance of the Cañadón del Irupé Fossils

The earliest South American record attributed to Marsileaceae may be the microspore *Crybelosporites berberioides* Burger, recorded in very low frequencies from Tithonian (uppermost Upper Jurassic) sediments of the Falkland (Malvinas) Plateau (Kotova 1983). It should be noted, however, that Batten et al. (1996) have since suggested that *Crybelosporites* is first definitively known from the Barremian (mid Early Cretaceous). The majority of the South American record of these spores is from Argentina, where *Crybelosporites* has been identified in the Upper Jurassic to Lower Cretaceous (Tithonian to Barremian) Springhill Formation of Tierra del Fuego (Del Fueyo et al. 2007); the Aptian to Albian La Cantera Formation of San Luis Province (Prámparo 1990, 1994); the Albian of the Kachaike and Lagarcito Formations of Santa Cruz and San Juan Provinces, respectively (Archangelsky and Llorens 2005; Prámparo et al. 2005; Del Fueyo et al. 2007; Villar de Seoane and Archangelsky 2008); and the Albian to Cenomanian of the Cañadón Seco Formation of Santa Cruz Province (Archangelsky et al. 1994). Later in the Cretaceous, *Crybelosporites* has been recorded from the Campanian to Maastrichtian of the La Colonia Formation (Cúneo et al. 2013) and the Maastrichtian of the Lefipán Formation (Baldoni 1992), Chubut Province; as well as from the Campanian to Maastrichtian of the Loncoche Formation, Mendoza Province (Puebla et al. in press). *Crybelosporites* is also known from the Albian of the Falkland (Malvinas) Plateau (Kotova 1983) and mid-Cretaceous sediments of Brazil (Herngreen 1973; De Lima 1982; Lupia et al. 2000) and Peru (Brenner 1968; Lupia et al. 2000). *Crybelosporites* has long been considered similar to spores of extant Marsileaceae, with at least some species thought to particularly resemble microspores produced by extant species of *Pilularia* and *Regnellidium* (Cookson and Dettmann 1958; Dettmann 1963; Lupia et al. 2000).

Although not included in previously published reviews of the fossil record of Marsileaceae, the microspore taxon *Gabonispuris* Boltenhagen is sometimes identified as representing dispersed marsileaceous microspores (e.g., Quattrocchio et al. 2000). These spores, particularly *Gabonispuris vigouroxii* Boltenhagen, are known from the Paleogene of Argentina, having been recovered from the Salta Group, Salta Province (Moroni 1982; Quattrocchio et al. 2000; Volkheimer et al. 2006), and the Bororó Formation of Chubut Province (Volkheimer et al. 2007). *Gabonispuris* is also known from the Late Cretaceous to Paleocene in other parts of South America, such as Bolivia (Vajda-Santivanez 1999) and Colombia (Garzon et al. 2012).

Megaspores assigned to the extinct genus *Arcellites*, which may have affinities to Marsileaceae (Ellis and Tschudy 1964; Collinson 1991, 1996; Batten et al. 1996, 2011; Lupia et al. 2006), have been found only in Santa Cruz Province, Argentina, reported from the Albian of the Kachaike and Piedra Clavada Formations (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, 2013) and also the Campanian to Maastrichtian of the Arcillas Fragmentosas Formation (Baldoni and Batten 1997). Baldoni and Batten (1997) suggested that the *Arcellites* isolated from Arcillas Fragmentosas Formation samples may have been introduced during sample preparation or may have been redeposited from more ancient sediments, making this occurrence suspect. The megaspore *Molaspora lobata* identified here from the Cañadón del Irupé locality has been documented only in one other locality, the Campanian to Maastrichtian Cerro Bosta locality of the La Colonia Formation of Chubut Province (Cúneo et al. 2013).

The South American marsileaceous macrofossil record includes only two previously known occurrences. The first is a report of macrofossil remains from the Maastrichtian Serra da Galga Member of the Marília Formation, Minas Gerais, Brazil; these were said to be sporocarps possibly representing *Marsilea* and were briefly described in an abstract (Senra and Silva e Silva 1998; see Candeiro et al. 2008 for further information on the locality). Cúneo et al. (2013) later described *Regnellidium thomas-taylorii* from the Cerro Bosta and Quebrada del Helecho localities of the La Colonia Formation. These fossils include rhizomes bearing roots, leaves with two leaflets, and a putative sporocarp.

The marsileaceous macrofossil remains from the Cañadón del Irupé locality include *Mirasolita irupensis* leaves and leaflets and *Lugiomarsiglia aquatica* sporocarps. The *Mirasolita* leaves have two leaflets, and the leaflets have a morphologically distinctive reniform, long-petiolulate shape, with a venation pattern most similar to that of extant species of *Marsilea*. The *Lugiomarsiglia* sporocarps, while certainly having affinities to Marsileaceae, are not unambiguously most similar to those borne by plants within any of the three extant genera. As with the *Regnellidium thomas-taylorii* macrofossils previously documented from the La Colonia Formation (Cúneo et al. 2013), the Cañadón del Irupé macrofossil material co-occurs with *Molaspora lobata* megaspores, which show only minor differences with megaspores produced by the extant species *Regnellidium diphyllum* (Dijkstra 1959; Lupia et al. 2000; Batten et al. 2011). The Cañadón del Irupé and Cerro Bosta megaspores are presently the only documented occurrences of *Molaspora* in South America, and among only a few occurrences of *Molaspora*/*Regnellidium*-like megaspores

documented from Gondwanan landmasses, with these megaspores being additionally recorded from the Albian to Cenomanian of Victoria, Australia (Douglas 1973; Tosolini et al. 2002, 2012); the Maastrichtian to Paleocene of Andhra Pradesh (Sarma 1947; age after Prasad et al. 1994) and Madya Pradesh (Sahni and Rao 1943; Sahni in Sahni and Sitholey 1943; Dijkstra 1959; Chitaley and Paradkar 1972; age after Kumaran et al. 1997), India; and possibly the Cretaceous of Egypt (Dijkstra 1959).

While the Cañadón del Irupé megaspores were not macerated directly from the sporocarps, it is reasonable to assume that the megaspores were produced by the marsileaceous plant or plants represented by the macrofossil remains from Cañadón del Irupé due to the fact that the macrofossils and microfossils can independently be attributed to Marsileaceae and co-occur in the same sediments. Additionally, the sporangia in the sporocarps are circular to slightly obovate in outline, similar to the shape of the *Molaspora* megaspores in the same sediments. This is significant because in extant Marsileaceae the capsule of the megasporangium roughly conforms to the shape of the sole megaspore it contains (Schneider and Pryer 2002). Finally, the maximum size of the *Lugiomarsiglia* sporangia exceeds the size of the dispersed megaspores, meaning the megaspores could plausibly have been accommodated within some of the sporangia.

The Cañadón del Irupé material provides further evidence that *Molaspora/Regnellidium*-type megaspores may have been produced by marsileaceous plants with a variety of morphologies in the Cretaceous, not just those with morphology consistent with extant *Regnellidium*. *Molaspora lobata*-like megaspores occur within *Marsilea*-like sporocarps of the *Rodeites* plant from India (Chitaley and Paradkar 1972; Paradkar and Barlinge 1981; Nagalingum 2007), which has leaves with six leaflets (Paradkar and Barlinge 1981) and *Marsilea*-like microspores (Lupia et al. 2000). *Molaspora* megaspores are also known to co-occur dispersed in the same sediments that bear marsileaceous fossil leaves with four leaflets, including at the Cenomanian Devils Kitchen locality, Eumeralla Formation, Victoria, Australia (*Molaspora lobata*: Tosolini et al. 2002, 2012; Nagalingum 2007), and with the *Marsileaceaphyllum johnhallii* plant from Cenomanian sediments of the Dakota Formation, Kansas, USA (*M. lobatum* and *M. salinum* Kovach & Dilcher: Kovach and Dilcher 1988; Skog and Dilcher 1992). It should be noted, however, that the possibly marsileaceous megaspore taxon *Arcellites* also occurs in the Eumeralla (Tosolini et al. 2002) and Dakota (Kovach and Dilcher 1988) Formations. Finally, *M. lobata* was recently reported co-occurring with macrofossils assigned to the genus *Regnellidium* at the Cerro Bosta locality of the La Colonia Formation (Cúneo et al. 2013).

Using the characteristics differentiating the megaspores of extant Marsileaceae as outlined by Lupia et al. (2000, Table 1) and Schneider and Pryer (2002, Table 3) as a guide, we thus predict that the ancestral megaspore type for extant Marsileaceae had a spheroidal shape, baculate sculpture, and a six-lobed, contorted acrolamella (=“solid acrolamella” of Schneider and Pryer 2002) like that of *Molaspora lobata* and extant *Regnellidium diphyllum*. Some of these characters—such as the spheroidal megaspore body and contorted, six-lobed acrolamella—may have evolved earlier than others if the megaspore taxon *Arcellites* is indeed corroborated to have been produced by an even earlier-evolved group with affinities to Marsileaceae, as suggested by Collinson (1991, 1996). In fact, Lupia et al. (2000) have proposed that the type of acrolamella seen in *Arcellites*, *Molaspora*, and *Regnellidium* could be a synapomorphy for extant Marsileaceae and related extinct taxa. We hypothesize that prolate megaspores with reticulate sculpture and a straight acrolamella (*Pilularia*) or an unlobed, highly reduced discoid (*Marsilea*) acrolamella evolved separately in the ancestors to extant *Pilularia* and *Marsilea*, respectively. The evolution of the macromorphology of the clade of extant Marsileaceae and its stem lineage continues to be difficult to reconstruct, in part due to the paucity of the macrofossil record.

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References

- Albino AM (2000) New record of snakes from the Cretaceous of Patagonia (Argentina). *Geodiversitas* 22:247–253
- Alonso Paz E, Bassagoda MJ (2002) Revisión de las Marsileaceae del Uruguay y primera cita de *Pilularia americana* A. Braun. *Comunicaciones Botánicas Museos Nac Historia Nat Antropolog* 125:1–8

- Archangelsky A, Llorens M (2005) Palinología de la Formación Kachaike, Cretácico Inferior de la Cuenca Austral, provincia de Santa Cruz. II. Esporas. *Ameghiniana* 42:311–328 (versión Online)
- Archangelsky S, Bellosi ES, Jalfin GA, Perrot C (1994) Palynology and alluvial facies from the mid-Cretaceous of Patagonia, subsurface of San Jorge Basin, Argentina. *Cretac Res* 15: 127–142
- Archangelsky A, Phipps CJ, Taylor TN, Taylor EL (1999) *Paleoazolla*, a new heterosporous fern from the Upper Cretaceous of Argentina. *Am J Bot* 86:1200–1206
- Ar dolino A, Delpino D (1987) Senoniano (continental-marino), Comarca Nordpatagónica Provincia de Chubut, Argentina. Décimo Congreso Geológico Argentino, San Miguel de Tucumán. *Actas* 3:193–196
- Baldoni AM (1987) Dos nuevas especies de megasporas de la Formación Kachaike, Cretácico Inferior de Santa Cruz, Argentina. *Anais X Congreso Brasil Paleontología*, Rio de Janeiro, pp 669–689
- Baldoni AM (1992) Palynology of the Lower Lefipán Formation (Upper Cretaceous) of Barranca de Los Perros, Chubut Province, Argentina. Part I. Cryptogam spores and gymnosperm pollen. *Palynol* 16:117–136
- Baldoni AM, Batten DJ (1997) Cretaceous megasporas from two boreholes in the Austral Basin, Santa Cruz Province, Argentina, and their stratigraphic and palaeoenvironmental significance. *Neues Jahrb Geol Paläontol* 205:97–110
- Baldoni AM, Taylor TN (1988) Ultraestructura de una nueva especie de *Arcellites* en el Cretácico Inferior de la provincia de Santa Cruz, Argentina y sus vinculaciones con la familia Marsileaceae. IV Congreso Argentino de Paleontología y Bioestratigrafía, Mendoza, Noviembre 23–27, 1986. *Actas* 3:15–19 (plates 1–3)
- Baldoni AM, Askin RA, Ragona D (2001) Palynology of the Lower Cretaceous Kachaike Formation, Santa Cruz Province, Argentina. In: *Proceedings of the IX International Palynological Congress*, Houston, 1996, pp 191–200
- Banerji J (1987) Further contribution to the Mesozoic flora of Kutch, Gujarat. *Geophytology* 17:64–74 (plate 1)
- Batten DJ (1988) Revision of S.J. Dijkstra's Late Cretaceous megasporas and other plant microfossils from Limburg, The Netherlands. *Meded Rijks Geol Dienst* 41–3:1–55
- Batten DJ, Collinson ME (2001) Revision of species of *Minerisporites*, *Azolla* and associated plant microfossils from deposits of the upper Palaeocene and Palaeocene/Eocene transition in The Netherlands, Belgium and the USA. *Rev Palaeobot Palynol* 115:1–32
- Batten DJ, Kovach WL (1990) Catalog of Mesozoic and Tertiary megasporas. *Am Assoc Stratigr Palynol Contrib Ser* 24:1–227
- Batten DJ, Dutta RJ, Knobloch E (1996) Differentiation, affinities and palaeoenvironmental significance of the megasporas *Arcellites* and *Bohemisporites* in Wealden and other Cretaceous successions. *Cretac Res* 17:39–65
- Batten DJ, Colin J, Néraudeau D (2010) Megasporas from mid Cretaceous deposits in western France and their biostratigraphic and palaeoenvironmental significance. *Rev Palaeobot Palynol* 161:151–167
- Batten DJ, Collinson ME, Brain APR (2011) Megasporas and microspores of the extant and Paleogene marsileaceous fern *Regnellidium* and Cretaceous *Molaspora*: evolutionary and phytogeographic implications. *Int J Plant Sci* 172:1087–1100
- Bilderback DE (1978) The development of the sporocarp of *Marsilea vestita*. *Am J Bot* 65:629–637
- Bingham PS, Savrda CE, Knight TK, Lewis RD (2008) Character and genesis of the Ingersoll Shale, a compact continental fossil-lagerstätte, Upper Cretaceous Eutaw Formation, eastern Alabama. *Palaios* 23:391–401
- Bonaparte JF (1985) A horned Cretaceous carnosaur from Patagonia. *Natl Geogr Res* 1:149–151
- Brenner GJ (1968) Middle Cretaceous spores and pollen from northeastern Peru. *Pollen Spores* 10:341–383
- Candeiro CRA, Santos AR, Bergqvist LP, Ribeiro LCB, Apesteuguía S (2008) The Late Cretaceous fauna and flora of the Uberaba area (Minas Gerais State, Brazil). *J S Am Earth Sci* 25:203–216
- Chitaley SD, Paradkar SA (1971, issued 1973) *Rodeites* Sahni reinvestigated—II. *Palaeobot* 20:293–296 (plate 1)
- Chitaley SD, Paradkar SA (1972) *Rodeites* Sahni reinvestigated—I. *Bot J Linn Soc* 65:109–117
- Collinson ME (1991) Diversification of modern heterosporous peridophytes. In: S Blackmore, SH Barnes (eds) *Pollen and spores. Systematics Association Special Volume No. 44*. Clarendon Press, Oxford, pp 119–150
- Collinson ME (1996) “What use are fossil ferns?”—20 years on: with a review of the fossil history of extant pteridophyte families and genera. In: Camus JM, Johns RJ (eds) *Pteridology in perspective*. Royal Botanic Gardens, Kew, pp 349–394
- Cookson IC, Dettmann ME (1958) Cretaceous “megasporas” and a closely associated microspore from the Australian region. *Micropaleontol* 4:39–49
- Cúneo NR, Hermsen EJ, Gandolfo MA (2013) *Regnellidium* macrofossils and associated spores from the Late Cretaceous of South America. *Int J Plant Sci* 174:340–349
- De Lima MR (1982) Palinología da Formação Codó na Região de Codó, Maranhão. *Bol IG Inst Geosci Univ São Paulo* 13:43–134
- Del Fueyo GM, Villar de Seoane L, Archangelsky A, Guler V, Llorens M, Archangelsky S, Gamero JC, Musacchio EA, Passalia MG, Barreda VD (2007) Biodiversidad de las paleofloras de Patagonia austral durante el Cretácico Inferior. *Asociación Paleontológica Argentina. Publ Espec* 11:101–122
- Dettmann ME (1963) Upper Mesozoic microfloras from south-eastern Australia. *Proc R Soc Vic* 77:1–148
- Dijkstra SJ (1959, issued 1961) On megasporas, Charophyta fruits and some other small fossils from the Cretaceous. *Palaeobot* 8: 8–18 (plates 1–2)
- Dorofeev PI (1963) Tertiary plants of Kazakhstan. *Bot Zhurnal* 48:171–181 (in Russian)
- Dorofeev PI (1981) On the taxonomy of the Tertiary Marsileaceae. *Bot Zhurnal* 66: 792–801 (plates 4–7, [in Russian])
- Dorofeev PI, Velichkevich FYu (1971) On *Pilularia* fossils in Byelorussia. *Dokl Akad Nauk Beloruss SSR* 15:169–172
- Douglas JG (1973) The Mesozoic floras of Victoria, part 3. Geological Survey of Victoria Memoir 29
- Ellis CH, Tschudy RH (1964) The Cretaceous megaspore genus *Arcellites* Miner. *Micropaleontol* 10:73–79
- Ellis B, Daly DC, Hickey LJ, Johnson KR, Mitchell JD, Wilf P, Wing SL (2009) *Manual of leaf architecture*. Comstock Publishing Associates, Cornell University Press, Ithaca, New York
- Fedotov VV (1978) *Regnellidium* (Marsileaceae) in the late Eocene flora of Rajchiha in Amur Region. *Bot Zhurnal* 63:589–593 (1 plate)
- Gandolfo, MA, Cúneo NR, Hermsen EJ (in press) Reporte preliminar sobre la paleoflora de la Formación La Colonia (Campaniano-Maastrichtiano, Cretácico tardío), Chubut, Patagonia, Argentina. *Bol Soc Geol Mex*
- Gandolfo MA, Cúneo NR (2005) Fossil Nelumbonaceae from the La Colonia Formation (Campanian–Maastrichtian, Upper Cretaceous), Chubut, Patagonia, Argentina. *Rev Palaeobot Palynol* 133:169–178
- García Massini JL, Jacobs BF, Tabor NJ (2010) Paleobotany and sedimentology of late Oligocene terrestrial strata from the northwestern Ethiopian Plateau. *Palaeontol Electron* 13.1.6A: 51
- Garzon S, Warny S, Bart PJ (2012) A palynological and sequence-stratigraphic study of Santonian–Maastrichtian strata from the

- Upper Magdalena Valley basin in central Colombia. *Palynol* 36:112–133
- Gasparini Z, De La Fuente M (2000) Tortugas y plesiosaurios de la Formación La Colonia (Cretácico superior) de Patagonia, Argentina. *Revista Esp Paleontol* 15:23–25
- Gasparini Z, Casadio S, Fernández M, Salgado L (2001) Marine reptiles from the Late Cretaceous of northern Patagonia. *J S Am Earth Sci* 14:51–60
- Gaudet JJ (1964) Morphology of *Marsilea vestita*. II. Morphology of the adult land and submerged leaves. *Am J Bot* 51:591–597
- Gupta KM (1962) *Marsilea*. *Bot Monogr* 2:1–109
- Hasebe M, Wolfe PG, Pryer KM, Ueda K, Ito M, Sano R, Gastony GJ, Yokoyama J, Manhart JR, Murakami N, Crane EH, Haufler CH, Hauk WD (1995) Use of molecular data in evolutionary studies of pteridophytes. *Am Fern J* 85:134–181
- Herman AB, Kvaček J (2007) Early Campanian Grünbach flora of Austria: systematic composition and palaeoclimatic interpretations. *Acta Palaeobot* 47:37–55
- Herman AB, Kvaček J (2010) Late Cretaceous Grünbach flora of Austria. *Naturhistorisches Museum Wien, Vienna*
- Herngreen GFW (1973) Palynology of Albian-Cenomanian strata of Borehole 1-QS-1-Ma, state of Maranhao, Brazil. *Pollen Spores* 15:515–555
- Hu S, Taylor DW, Brenner GJ, Basha SH (2008) A new marsilealean fern species from the Early Cretaceous of Jordan. *Palaeoworld* 17:235–245
- Jacono CC, Johnson DM (2006) Water-clover ferns, *Marsilea*, in the southeastern United States. *Castanea* 71:1–14
- Johnson DS (1898) On the development of the leaf and sporocarp in *Marsilea quadrifolia* L. *Ann Bot* 12:119–145 (plates 10–12)
- Johnson DM (1986) Systematics of the New World species of *Marsilea* (Marsileaceae). *Syst Bot Monogr* 11:1–87
- Kawamura H (2010) Stratigraphic revision of the Jurassic Toyora Group of the southern part of the Tabe Basin, Yamaguchi Prefecture, southwest Japan. *J Geol Soc Jpn* 116:27–44 (in Japanese with English abstract)
- Kielan-Jaworowska Z, Ortiz-Jaureguizar E, Vieytes C, Pascual R, Goin FJ (2007) First ?cimolodontan multituberculate mammal from South America. *Acta Palaeontol Polonica* 52:257–262
- Kotova IZ (1983) Palynological study of Upper Jurassic and Lower Cretaceous sediments, Site 511, Deep Sea Drilling Project Leg 71 (Falkland Plateau). *Deep Sea Drilling Program Initial Rep* 71:879–906
- Kovach WL, Batten DJ (1989) Worldwide stratigraphic occurrences of Mesozoic and Tertiary megaspores. *Palynol* 13:247–277
- Kovach WL, Dilcher DL (1988) Megaspores and other dispersed plant remains from the Dakota Formation (Cenomanian) of Kansas, USA. *Palynol* 12:89–119
- Kramer KU (1990) Marsileaceae. In: Kubitzki K, Green PS (eds) *The families and genera of vascular plants. I. Pteridophytes and gymnosperms*. Springer, Berlin, pp 180–183
- Krasser F (1906) Über die fossile Kreideflora von Grünbach in Niederösterreich. *Anz Kais Akad Wiss Math-Naturwissenschaftliche Kl* 43:41–43
- Kumaran KPN, Bonde SD, Kanitkar MD (1997) An *Aquilapollenites*-associated palynoflora from Mohgaonkalan and its implication for age and stratigraphic correlation of Deccan Intertrappean beds. *Curr Sci* 72:590–592
- Kvaček J, Herman A (2004) The Campanian Grünbach flora of Lower Austria: palaeoecological interpretations. *Ann Naturhistorischen Mus Wien* 106A:91–101
- Lavver DR, Debee AM, Clarke JA, Rougier GW (2011) A new enantiornithine bird from the Upper Cretaceous La Colonia Formation of Patagonia, Argentina. *Ann Carnegie Mus* 80:35–42
- Lupia R, Schneider H, Moeser GM, Pryer KM, Crane PR (2000) Marsileaceae sporocarps and spores from the Late Cretaceous of Georgia, USA. *Int J Plant Sci* 161:975–988
- Lupia R, Schneider H, Nagalingum NS, Pryer KM (2006) Jurassic origin for the Salviniaceae: the last word or just the first? *Botany* 2006, 28 July–2 August, Chico, California: Abstract ID 535
- Mahabalé TS (1956) Trends of specialization in the sporocarp and spores in the living and fossil Marsileaceae. *Palaeobot* 5:66–72 (plates 1–2)
- Moroni AM (1982) Correlación palinológica en las formaciones Olmedo y Yacoraite. Cuenca del noroeste Argentino. III Congreso Geológico Chileno, Concepción, 8–14 Noviembre, 1982. *Actas: F 339-F 349*
- Nagalingum NS (2007) *Marsileaceaphyllum*, a new genus for marsileaceous macrofossils: leaf remains from the Early Cretaceous (Albian) of southern Gondwana. *Plant Syst Evol* 264:41–55
- Nagalingum NS, Schneider H, Pryer KM (2006) Comparative morphology of reproductive structures in heterosporous water ferns and a reevaluation of the sporocarp. *Int J Plant Sci* 167:805–815
- Nagalingum NS, Schneider H, Pryer KM (2007) Molecular phylogenetic relationships and morphological evolution in the heterosporous fern genus *Marsilea*. *Syst Bot* 32:16–25
- Nagalingum NS, Nowak MD, Pryer KM (2008) Assessing phylogenetic relationships in extant heterosporous ferns (Salvinales), with a focus on *Pilularia* and *Salvinia*. *Bot J Linn Soc* 157:673–685
- O’Gorman JP, Gasparini Z (2013) Revision of *Sulcusuchus errani* (Sauropterygia, Polycotyliidae) from the Upper Cretaceous of Patagonia, Argentina. *Alcheringa* 37:163–176
- O’Gorman JP, Salgado L, Cerda IA, Gasparini Z (2012) First record of gastroliths associated with elasmosaur remains from La Colonia Formation (Campanian-Maastrichtian), Chubut, Patagonia Argentina, with comments on the probable depositional palaeoenvironment of the source of the gastroliths. *Cretac Res* 40:212–217
- Paradkar SA, Barlinge SG (1981) *Rodeites* revisited—III. Geophytology 11:16–24 (plate 1)
- Pascual R, Goin FJ, González P (2000) A highly derived docodont from the Patagonian Late Cretaceous: evolutionary implications for Gondwana mammals. *Geodiversitas* 22:395–414
- Prámparo MB (1990) Palynostratigraphy of the Lower Cretaceous of the San Luis Basin, Argentina. Its place in the Lower Cretaceous flora provinces pattern. *Neues Jahrb Geol Paläontol Abh* 181:255–266
- Prámparo MB (1994) Lower Cretaceous palynoflora of the La Cantera Formation, San Luis Basin: correlation with other Cretaceous palynofloras of Argentina. *Cretac Res* 15:193–203
- Prámparo MB, Ballent SC, Gallego OF, Milana JP (2005) Paleontología de la Formación Lagarcito (Cretácico inferior) en la provincia de San Juan, Argentina. *Ameghiniana* versión On-line 42:93–114
- Prasad GVR, Jaeger JJ, Sahni A, Gheerbrant E, Khajuria CK (1994) Eutherian mammals from the Upper Cretaceous (Maastrichtian) Intertrappean Beds of Naskal, Andhra Pradesh, India. *J Vertebr Paleontol* 14:260–277
- Pray TR (1962) Ontogeny of the closed dichotomous venation of *Regnellidium*. *Am J Bot* 49:464–472
- Pryer KM (1999) Phylogeny of marsileaceous ferns and relationships of the fossil *Hydropteris pinnata* reconsidered. *Int J Plant Sci* 160:931–954
- Pryer KM, Hearn DJ (2009) Evolution of leaf form in marsileaceous ferns: evidence for heterochrony. *Evol* 63:498–513

- Puebla GG, Prámparo MB, Gandolfo MA (in press) Late Cretaceous aquatic ferns from Mendoza, central-western Argentina. *Int J Plant Sci*
- Quattrocchio M, Ruiz L, Volkheimer W (2000) Palynological zonation of the Paleogene of the Colorado and Salta Group Basins, Argentina. *Revista Esp Micropaleontol* 32:61–78
- Rai J (2006) Discovery of nanofossils in a plant bed of the Bhuj Member, Kutch and its significance. *Curr Sci* 91:519–526
- Reveal, JL (2009–2012) Indices Nominum Supergenericorum Plantarum Vascularium. <http://www.plantsystematics.org/reveal/pbio/fam/allspgnames.html>. Accessed 2 July 2013
- Rich FJ, Johnson DM, Durkin TV (2001) Occurrence and paleoecology of *Marsilea* from the Eocene Wasatch Formation, Johnson County, Wyoming. *Palaos* 16:608–613
- Rothwell GW (1999) Fossils and ferns in the resolution of land plant phylogeny. *Bot Rev* 65:188–218
- Rothwell GW, Stockey RA (1994) The role of *Hydropteris pinnata* gen. et sp. nov. in reconstructing the cladistics of heterosporous ferns. *Am J Bot* 81:479–492
- Rougier GW, Forasiepi AM, Hill RV, Novacek M (2009) New mammalian remains from the Late Cretaceous La Colonia Formation, Patagonia, Argentina. *Acta Palaeontol Polonica* 54:195–212
- Sahni B, Rao HS (1943) A silicified flora from the intertrappean cherts round Sausar in the Deccan. *Proc Natl Acad Sci India* 13:36–75
- Sahni B, Sitholey RV (1943) Palaeobotany in India IV. Progress report for 1942. *J Indian Bot Soc* 22:182 (plates 6–9)
- Sarma SR (1947) A note on the occurrence of spores comparable to *Rodeites dakshini* Sahni from the Deccan Intertrappean beds of Vikarabad. *Curr Sci* 16:338
- Schneider H, Pryer KM (2002) Structure and function of spores in the aquatic heterosporous fern family Marsileaceae. *Int J Plant Sci* 163:485–505
- Senra MCE, Silva e Silva LH (1998) Presença de pteridófitas na Formação Marília, Grupo Bauru, Cretáceo Superior de Minas Gerais. *Anais Academia Bras Cienc* 70:380–381
- Seward AC (1910) *Fossil Plants*, vol II. Cambridge University Press, Cambridge
- Skog JE, Dilcher DL (1992) A new species of *Marsilea* from the Dakota Formation in central Kansas. *Am J Bot* 79:982–988
- Skog JE, Dilcher DL (1994) Lower vascular plants of the Dakota Formation in Kansas and Nebraska, USA. *Rev Palaeobot Palynol* 80:1–18
- Smith AR, Pryer KM, Schuettpelz E, Korall P, Schneider H, Wolf PG (2006) A classification for extant ferns. *Taxon* 55:705–731
- Sterli J, De la Fuente MS (2011) A new turtle from the La Colonia Formation (Campanian-Maastrichtian), Patagonia, Argentina, with remarks on the evolution of the vertebral column in turtles. *Palaeontol* 54:63–78
- Sweet AR (1979) Jurassic and Cretaceous megaspores. *Am Assoc Stratigr Palynol Contrib Ser* 5B:1–30
- Tosolini AMP, McLoughlin S, Drinnan AN (2002) Early Cretaceous megaspore assemblages from southeastern Australia. *Cretac Res* 23:807–844
- Tosolini AMP, Wagstaff BE, Cantrill DJ, Hills RAE, Gallaher SJ (2012) Early Cretaceous angiosperms of southeastern Australia—no longer early. *Jpn J Palynol* 58 (Special Issue, Abstracts: IPC/IOPC 2012): 239
- Tryon RM, Tryon AF (1982) *Ferns and allied plants*. Springer, New York
- Vajda-Santivanez V (1999) Miospores from Upper Cretaceous-Paleocene strata in northwestern Bolivia. *Palynol* 23:181–196
- Villar de Seoane L, Archangelsky S (2008) Taxonomy and biostratigraphy of Cretaceous megaspores from Patagonia, Argentina. *Cretac Res* 29:354–372
- Villar de Seoane L, Archangelsky S (2013) Ultrastructural study of *Arcellites humilis* Villar de Seoane and Archangelsky, 2008, from the Cretaceous of Patagonia, Argentina. *Geobios* 46:243–252
- Volkheimer W, Novara MG, Narváez PL, Marquillas RA (2006) Palynology and paleoenvironmental significance of the Tunal Formation (Danian) at its type locality, El Chorro Creek (Salta, Argentina). *Ameghiniana versión On-line* 43:567–584
- Volkheimer W, Scafati L, Melendi DL (2007) Palynology of a Danian warm climatic wetland in central northern Patagonia, Argentina. *Revista Esp Micropaleontol* 39:117–134
- Wagner WH (1952) Types of foliar dichotomy in living ferns. *Am J Bot* 39:578–592
- Yamada T, Kato M (2002) *Regnellites nagashimae* gen. et sp. nov., the oldest macrofossil of Marsileaceae, from the Upper Jurassic to Lower Cretaceous of western Japan. *Int J Plant Sci* 163:715–723
- Yamada T, Ohno T (2005) Revision of the stratigraphy of the Toyora and Toyonishi Groups in the Ouchi-Kikugawa area, Yamaguchi Prefecture, west Japan. *J Geol Soc Jpn* 111:389–403