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A new isoetalean microsporophyll from the latest Albian of northeastern Spain: Diversity in the development and dispersal strategies of microspores

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In this paper well-preserved isoetalean microsporophyll, containing in situ microspores, is described from the uppermost part of the Utrillas Formation (latest Albian) in Teruel Province, northeastern Spain. Similar but dispersed microspores were described previously as *Peromonolites*. Fossil plant impressions and compressions including the sporophyll lamina and microsporangium are referred to the fossil genus *Isoetites*. Although *Isoetes*-like megafossil remains, often with in situ or associated megaspores, are known from quite a few Cretaceous sites, and dispersed microspores are known, the presence of intact microsporangia is rare. Herein we suggest that microsporangia may have dispersed in masses, possibly representing a new unknown strategy in microspore dispersal in this group of plants.

Key words: Lycophyta, Isoetales, *Isoetites*, *Peromonolites*, microsporophyll, Albian, Spain.

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Introduction

Modern Isoetaceae have worldwide distribution, living in temperate-warm regions of all continents, from sea level to 4200 m, most frequently above 2000 m (Tryon and Tryon 1982). They usually occur in aquatic habitats or soils that are saturated with water at least part of the year (Tryon and Lugardon 1990). These heterosporous plants are typically small herbs with simple clusters of quill-like leaves, with sporangia (bearing either megaspores or microspores in separate sporangia). Each sporangium is attached to the inner base of most mature leaves. The microspores of living *Isoetes* are freely dispersed when they become mature. The fossil genus *Isoetites* was erected by Münster (1842) to describe fossil plants that have certain characters that suggest a relationship to extant *Isoetes*, but which differs in stem or leaf morphology, or in which some plant part is lacking. However, compressions of sporophylls, which may be isolated or attached to cormlike stems, have been included in *Isoetites* (Skog et al. 1992: 151). Most of the authors indicate that there is no clear distinction recognizable between *Isoetites* and *Isoetes*. However, recently Kustatscher et al. (2010: 601) suggested that the genus *Isoetes* should not be used if all the characters of this extant genus are not present. Furthermore, Kustatscher et al. (2010: 601) emended the genus *Isoetites* to include "Herbaceous lycophyte with lanceolate to elongate leaves, expanded basally, bearing mega- and microsporangia. Stem from reduced (almost missing) to short; corm unlobed or slightly lobed. Several to many ligulate sporophylls, erect to

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spreading. Megasporangia on the outermost whorl of sporophylls, microsporangia on the more inner whorls. Leaves of the innermost whorls generally sterile. Megaspores globose and trilete, microspores elongated to reniform, monolete, smooth to sculptured."

Although the genus *Isoetites* is known as early as the Triassic (Kustatscher et al. 2010), during the Cretaceous, isoetaleans were herbaceous plants with corm-like rhizomorphs rarely reaching 18 cm in height (Pigg 1992). Isoetalean plants represented by entire corm-like structures and aggregations of sporophylls have been observed in the Early Cretaceous Santana Formation of Brazil (Dilcher et al. 2000), Aptian deposits of Tunisia (Barale 1999), Albian of Portugal (Saporta 1894; Teixeira 1948), and in the Early (Krassilov 1982) and Late Cretaceous (Krassilov and Makulbekov 1996) of Mongolia. Other fossils corresponding to *Isoetites* have also been reported from the Middle Jurassic of the United States (Ash and Pigg 1991), Jurassic and Early Cretaceous rocks of India (Banerji 1989; Bose and Roy 1964), the mid-Cretaceous Dakota Group of Kansas and Nebraska (Skog et al. 1992) and Paleocene–Eocene of western North America (Brown 1939; Pigg 2001), Wealden from the upper Ashdown Formation (Batten 2011) and ex situ material which is thought to be derived from the Wealden succession of England (Skog and Hill 1992).

For the Cretaceous in situ isoetalean megaspores have been described from isolated megasporophylls from the Upper Weald Clay (Barremian) at Smokejacks Brickworks in the United Kingdom (Jarzembowski et al. 1996) and the Early (Krassilov 1982) and Late Cretaceous (Krassilov and Makulbekov 1996) of Mongolia. Corms with attached roots and sporophylls with in situ isoetalean megaspores have been found from the Middle–Late Jurassic Bhuj Formation in India (Banerji 1989) and early Aptian Douiret Formation of Merbah el Asfer in Tunisia (Barale 1999). There are several contributions in which the megaspore genera *Paxillitriletes* and *Minerisporites* in particular are discussed in the context of attribution to the Isoetales (e.g., Collinson et al. 1985; Batten 1988; Collinson 1991; Kovach and Dilcher 1988; Skog et al. 1992; Kovach 1994; Batten and Collinson 2001; Batten et al. 2011). Some works show microspores adhering to sculptural elements of dispersed *Minerisporites* (Collinson et al. 1985; Collinson 1991; Batten and Collinson 2001) and *Paxillitriletes* (Lupia 2011). *Minerisporites marginatus* (Dijkstra, 1951) Potonié, 1956 was previously described from the Early Cretaceous of South Australia (Cookson and Dettmann 1958), the boreholes A and B in The Netherlands (Dijkstra 1951) and the Mons Basin in Belgium (Delcourt and Sprumont 1955; Yans 2003). This species was also found in the Peace River area in Canada together with *Minerisporites venustus* Singh, 1964 (Singh 1971), in Człuchów (Poland) together with *M. richardsoni* (Murray, 1939) Harris, 1961 (Waksmundzka 1982) and from the Wealden of the United Kingdom as cfB. *M. marginatus* with *M. alius* Batten, 1969 (Batten 1969). Dispersed megaspores of *Isoetites* of probable late Barremian–early Aptian age have been described in Torres Vedrás locality in Portugal (Friis et al. 2010). Some dispersed megaspores belonging to the genera *Paxillitriletes* and *Dijkstraisporites* from the Barremian of Brilon-Nehden, Germany, and the Patuxent Formation (Aptian–early Albian) of Virginia, USA, seem to be related to *Isoetes* (Hueber 1982; Wilde and Hemsley 2000; Friis et al. 2010). Megaspore-like structures from *Isoetites* sp. 2 have been noted from the top Ashdown Formation (Berriasian–Valanginian) near Hastings, in the United Kingdom (Jarzembowski et al. 1996).

The precise shape and structure of the fertile parts of ancient Isoetales are still poorly known (Grauvogel-Stamm and Lugardon 2001: 136). The present work yields new data on reproductive strategy and microspore dispersal of fossil isoetalean plants, and provides the first description of Mesozoic isoetalean microsporophyll with many in situ masses containing hundreds of microspores.

Institutional abbreviations.—MPZ, Museo Paleontológico de Zaragoza, Spain.

Geographic and geological setting

The studied material comes from a clay pit near the village of Estercuel (Teruel Province, northeastern Spain), located in the southwestern Aragonese branch of the Iberian Chain (Fig. 1).

The locality is in the Oliete Sub-basin (Soria 1997). Two levels can be differentiated based on sedimentological data. The beds bearing the studied isoetalean macroflora (level ET 2-1) correspond to grey claystone beds intercalated with medium-grained yellow sandstone and deposited in a tidally influenced fluvial sedimentary environment. This level also contains a very diverse and exceptionally well-preserved macro- and microfloral assemblages, which includes other isoetalean non-fertile leaves (Sender et al. 2012). The overlying level ET 2-2 corresponds to black claystone with marine bivalves and less abundant plant remains. Both levels correspond to the "Boundary Marls" unit (the "Margas de Transición" unit of Aguilar et al. 1971). This unit reflects the transition between the underlying fluvial sandstone of the Utrillas Formation and the overlying shallow marine limestone of the Mosqueruela Formation (Fig. 1). The age of this unit in Estercuel has been established as latest Albian on the basis of the palynological assemblage (Sender et al. 2012; Villanueva-Amadoz et al. 2011).

Previous studies on this unit in the nearby area of Plou, also located in the Oliete Sub-basin, have determined shallow lacustrine facies deposited with significant oscillation of the water table and occasionally with a fluvial influence dominated by hydrophytic plants. The lacustrine depositional basin was infilled with sediment, leading to a final colonization by terrestrial sun-loving or helophytic plants (Gomez et al. 2009; Sender et al. 2010). In Estercuel sedimentological studies suggest tidally influenced fluvial and

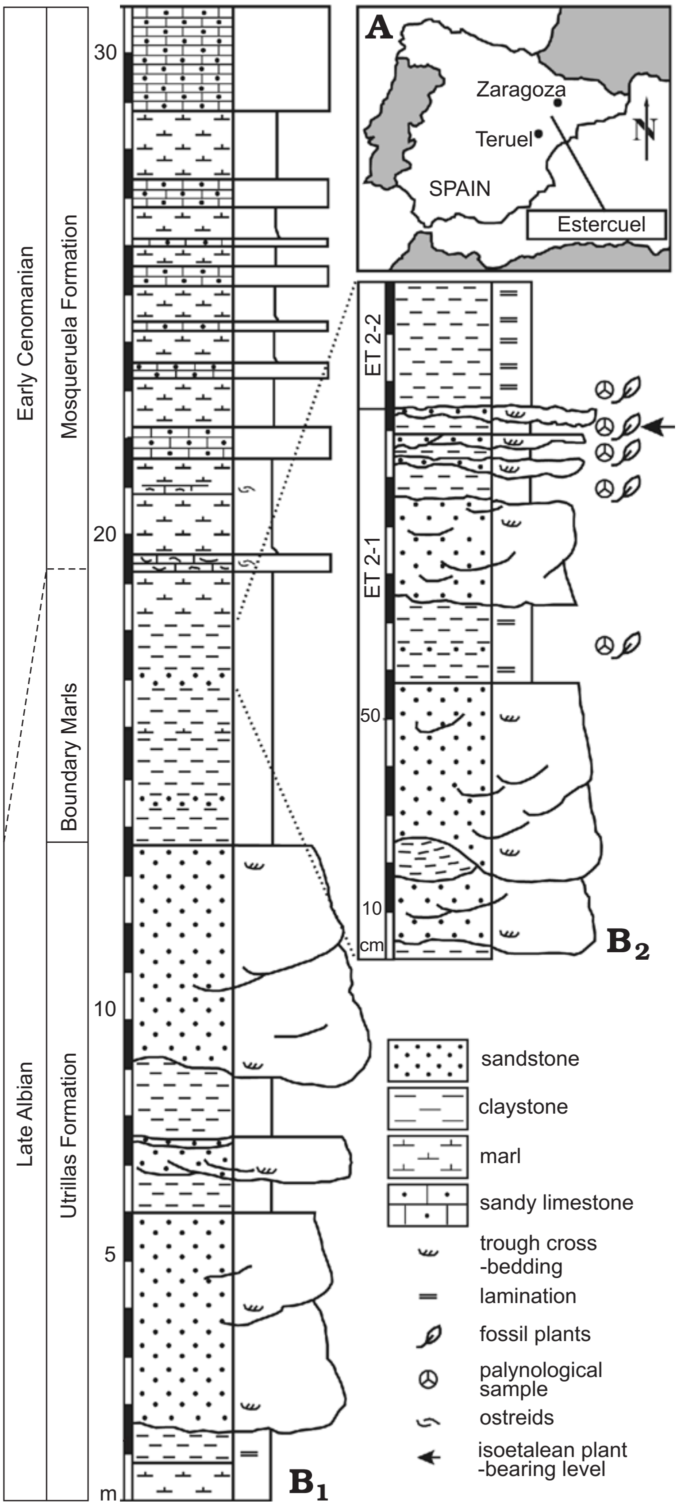

Fig. 1. **A.** Geographic location of the studied fossiliferous site of the Estercuel locality, northeast Spain. **B**. Stratigraphic sequence (modified from Pardo 1979) (B_1) and detailed log (B_2) with the stratigraphical level containing studied isoetalean material marked by a black arrow (level ET 2-1).

swampy environments with low marine input demonstrated by the presence of dinoflagellate cysts and mytiloid bivalves (Sender et al. 2012).

Material and methods

The studied fossil material (MPZ 2010/919) is preserved as impression and compression material (Figs. 2–4). We have assigned this material to the genus *Isoetites* following the emended diagnosis of Kustatscher et al. (2010) as it lacks some of the characters of the living genus *Isoetes*. It corresponds to a complete isolated microsporophyll bearing an attached basal sporangium (Fig. 2A, B, indicated as microsporangium in Fig. 2A) that contains in situ microspores grouped in masses (Figs. 2B_4 and 3A indicated by white arrows). Seven of these masses were recovered and prepared for study under SEM (Fig. 3B, D).

Observations were made with a stereoscopic light microscope, aided by scanning electron microscopy (SEM). Only SEM images were used for illustration of palynological material, because of the high magnification required to resolve micromorphology. For SEM observation the microspore masses were removed from the rock and handled with a moist brush without any chemical treatment, and placed on double-sided sticky tape on bronze stubs. The samples were coated with gold-palladium, and examined with a SEM Phillips XL 30 at the C.A.C.T.I. (University of Vigo, Spain).

Systematic palaeontology

Order Isoetales Prantl, 1874

Family Isoetaceae Reichenbach, 1828

Genus *Isoetites* (Münster 1842) emend. Kustatscher, Wachtler, and van Konijnenburg-van Cittert, 2010

Type species: *Isoetites crociformis* Münster, 1842 from the Late Jurassic of Solnhofen, Bavaria, Germany.

Isoetites sp.

Figs. 2A, B, 3A–D, 4A–E.

Material.—MPZ 2010/919, from Estercuel quarry, Teruel, northeastern Spain.

Description

Microsporophyll.—The leaf impression is simple, linear, about 22.1 mm long and 4.4 mm wide (Fig. 2A, B_1, B_2). The margin is entire, with its base slightly expanded and the apex acute. The leaf shows a large midvein up to 2 mm wide (Fig. 2A, indicated as central vein). The lamina is trabeculated, with trabeculae at intervals of about 1 mm (Fig. 2A, B_1, B_2, indicated by arrows in Fig. 2B_2). However, the presence of trabeculae (which would not be confused by horizontal lines appearing on the laminar surface of the sporophyll are related to air channels in extant and fossil *Isoetes* and related forms) inside the microsporangium is not evident possibly due to taphonomic biases (Fig. 2B_4). The impression of an elliptical ligule is preserved with an acute apex (Fig. 2A, B_1, B_3).

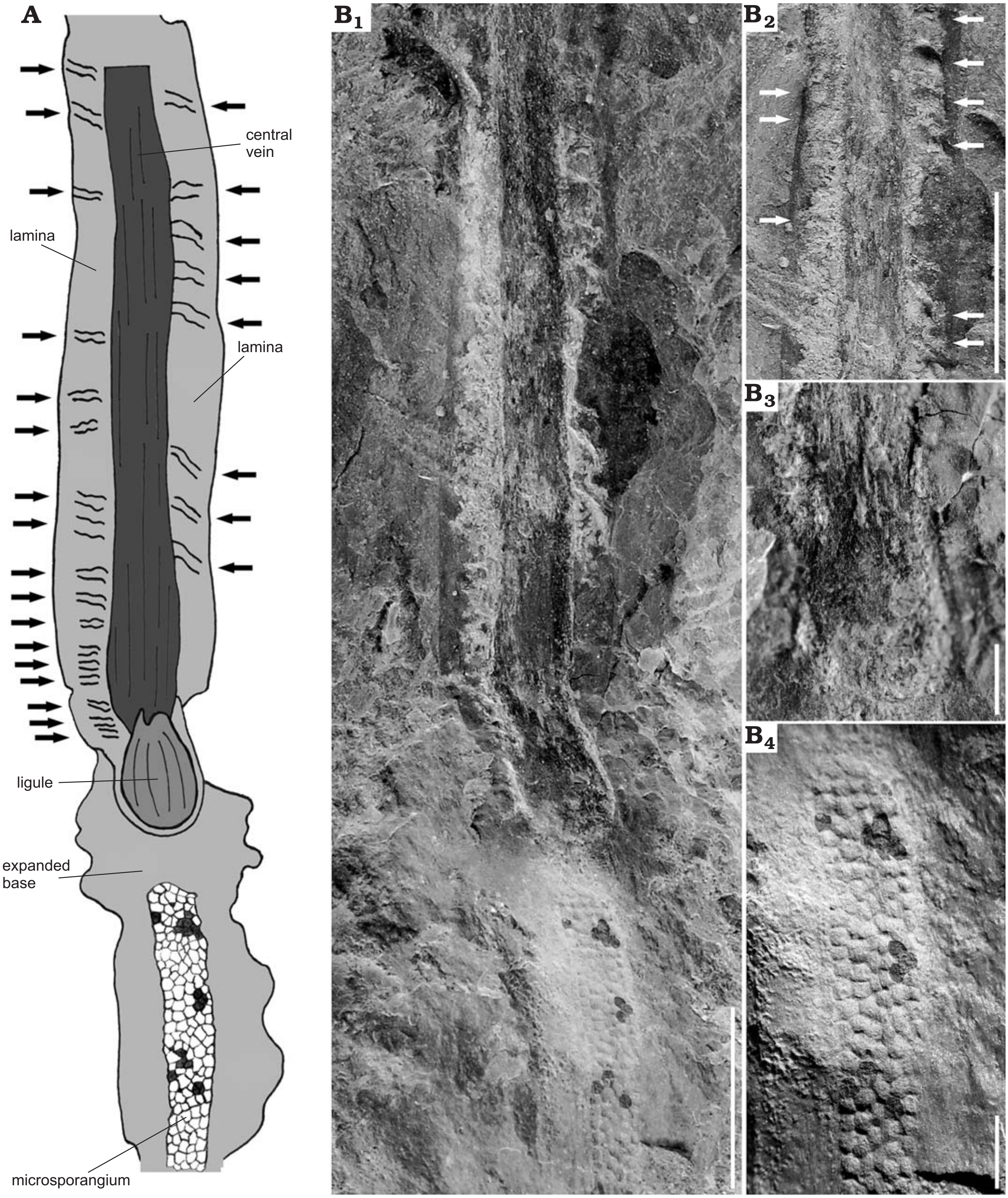

Fig. 2. Isoetalean microsporophyll with in situ masses of microspores, from the Boundary Marls unit (uppermost Albian) of Estercuel (Teruel, Spain). **A**. Explanatory drawing of the microsporophyll in B. Black arrows and the irregular lines indicate the impressions of trabeculae in leaf section. **B**. MPZ 2010/919. Microsporophyll with the sporangium at base containing masses of microspores (B_1). Detail of the microsporophyll lamina with impressions of trabeculae indicated by white arrows (B_2). Detail of the base of the microsporophyll leaf showing the impression of ligule (B_3). Microsporangium containing masses of microspores (B_4). Scale bars: A, B_1, B_2, 5 mm; B_3, B_4, 1 mm.

The base of the microsporophyll is spatulate proximally and oval distally (Fig. 2A, B_1). It measures 9.7 mm long and 2.5 mm wide and contains the elongate microsporangium (Fig. 2A, B_1, B_4). There is no evidence of a velum. The microsporangium contains a mesh of circa 135 polygonal bodies (Figs. 2A, B_1, B_4, 3A) of variable sizes (largest axes between 300 μm and 450 μm) and different morphologies with pentagonal or hexagonal shapes.

The masses are elliptical in shape, approximately 400–580 μm long and 290–320 μm wide, containing hundreds of microspores (Fig. 3B, D). The microspores seems to be grouped in tetrads (Fig. 3C, indicated by arrows).

Microspores (Figs. 3C, 4A–E).—Bilateral, plano-convex, monolete with a perinous layer and the straight laesura is well marked on almost the whole length of the proximal face, with elevated lips 2.6–4.5 μm high (Fig. 4D, E). Microspores are elliptic in polar view 20–34 μm long and 17–32 μm wide. Proximal and distal faces appear flattened due to compaction. A distinct feature of the microspore is a flange-like extension of the equatorial ridge 1.4–3.7 μm wide (Fig. 4A–E). On the proximal and distal face the perispore has a microgranulate micro-ornamentation (Fig. 4A–E). A characteristic tuberculate ornamentation occurs only on the distal face, with tubercles (0.1–2 μm high and 0.4–2 μm wide) spaced 0.2–4.9 μm apart and showing an apical more or less circular pit 0.1–1.6 μm in diameter (Figs. 3C, 4A, B). A cavate exine is 0.4 μm thick with a smooth inner layer of 0.1 μm and a tuberculate outer layer of 0.3 μm.

Remarks.—During the Triassic there is a change in isoetalean microspore apertures from trilete to monolete, a character related to modern-day *Isoetes* (Pigg 2001). Nonetheless, *Pleuromeia* Corda in Germar, 1852 (Glaessner and Rao 1955), *Lycostrobus* Nathorst, 1908 (Kempf 1971; Scott and Playford 1985) and *Lepacyclothes* Emmons, 1856 (formerly *Annalepis* Fliche, 1910 in Retallack 1997: 507) are other Triassic genera related to *Isoetites*, which have yielded in situ monolete microspores similar to *Aratrisporites* (Dettmann 1961; Retallack 1997; Grauvogel-Stamm and Lugardon 2001), showing this evolution. *Aratrisporites* microspores have also been found from *Tenellisporites* trilete megaspores (Fliche 1910; Grauvogel-Stamm and Duringer 1983). Moreover, Cretaceous genera *Nathorstiana* Richter, 1909, and *Nathorstianella* Glaessner and Rao, 1955 are also related to *Isoetites* (Kustatscher et al. 2010). There is a clear evolution trend from the Triassic *Pleuromeia*, through Cretaceous *Nathorstiana* and *Nathorstianella*, to *Isoetes* (Glaessner and Rao 1955). However, *Nathorstiana* and *Nathorstianella* have not yielded any reproductive structures within the fossil record to compare those microspores with the microspores presented herein.

Similarities between *Selaginella* and *Isoetes* have been established due to the similarities in wall structure of the microspores and megaspores, suggesting an old connection of these groups (Tryon and Lugardon 1990). However, the distinctive vegetative characters and the difference in aperture of the microspores (monolete in *Isoetes* and trilete in *Selaginella*) support the association of the studied fossil material with *Isoetes* rather than *Selaginella*.

Morphological characters of the here described in situ microspores, correspond most closely to the cavate genera *Peromonolites* Couper, 1953 and *Aratrisporites* Leschik, 1955. The original descriptions of both genera and emendation of the genus *Aratrisporites* (Klaus 1960: 145; Playford and Dettmann 1965: 151), are similar in terms of morphological characters. Microspores belonging to *Isoetes* are also morphologically similar to the fossil spores *Aratrisporites* (see illustrations in Harris 1955: pl. 2: 1, 2) and *Peromonolites* (see illustrations in Couper 1953: figs. 31, 32; 1960: pl. 2: 1). *Aratrisporites* has been used for Triassic and *Peromonolites* for Cretaceous–Cenozoic spores.

Initially, the genus *Peromonolites* was delimited for the Cretaceous by Couper (1953) as anisopolar, bilateral monolete (occasionally alete) spores with laesura occasionally indicated only by a weak area in the exine, surrounded by a sculptured perispore. In the diagnosis of this genus this author did not give any indication of the differences in the ornamentation on distal and proximal faces. Moreover, he described the type species *Peromonolites bowenii* Couper, 1953 as having sub-verrucate ornamentation of the central body in both faces, a hyaline psilate perispore, and as being distinct by its monolete aperture with a laesura extending the whole length of proximal face.

The first description of the genus *Aratrisporites* given by Leschik (1955) included zonate spinulose spores, however, this first description did not include any reference of the type of aperture, but was considered monolete by Klaus (1960). The latter emended the genus *Aratrisporites* stating that it was a gondola-shaped monolete spore, with granulate to spinulose sclerine, and zonate exine. Later, Playford and Dettmann (1965) emended the diagnosis of *Aratrisporites* and transferred it from the Subturma *Zonomonoletes* Luber, 1935 (Luber 1935) to Suprasubturma *Perinomonolites* Erdtman, 1947 (Erdtman 1947) on the grounds that it is cavate and not zonate. Playford and Dettmann (1965) also considered the genus *Saturnisporites* Klaus, 1960 a junior synonym of *Aratrisporites* (Leschik, 1955) Playford and Dettmann, 1965. They assumed that the characters of presence of elevated laesurate lips and the absence of typical anchor-shaped laesura in the polar ends, as described by Klaus (1960), were not diagnostic features for differentiating these genera. None of these authors gave any indication of differences in ornamentation of the sclerine between the proximal and distal faces in the description of the genus and type species, and it is difficult to observe in the original figures of Leschik (1955: pl. 5: 2, 4).

In situ microspores of *Aratrisporites* (probably *A. minimus* Schulz, 1967) have been described from Triassic microsporophylls of *Annalepis zeilleri* Fliche, 1910 (Grauvogel-Stamm and Duringer 1983), which are considered isoetalean lycopsids (Pigg 1992). The sculpture of those microspores are specified in the text as being infragranulate

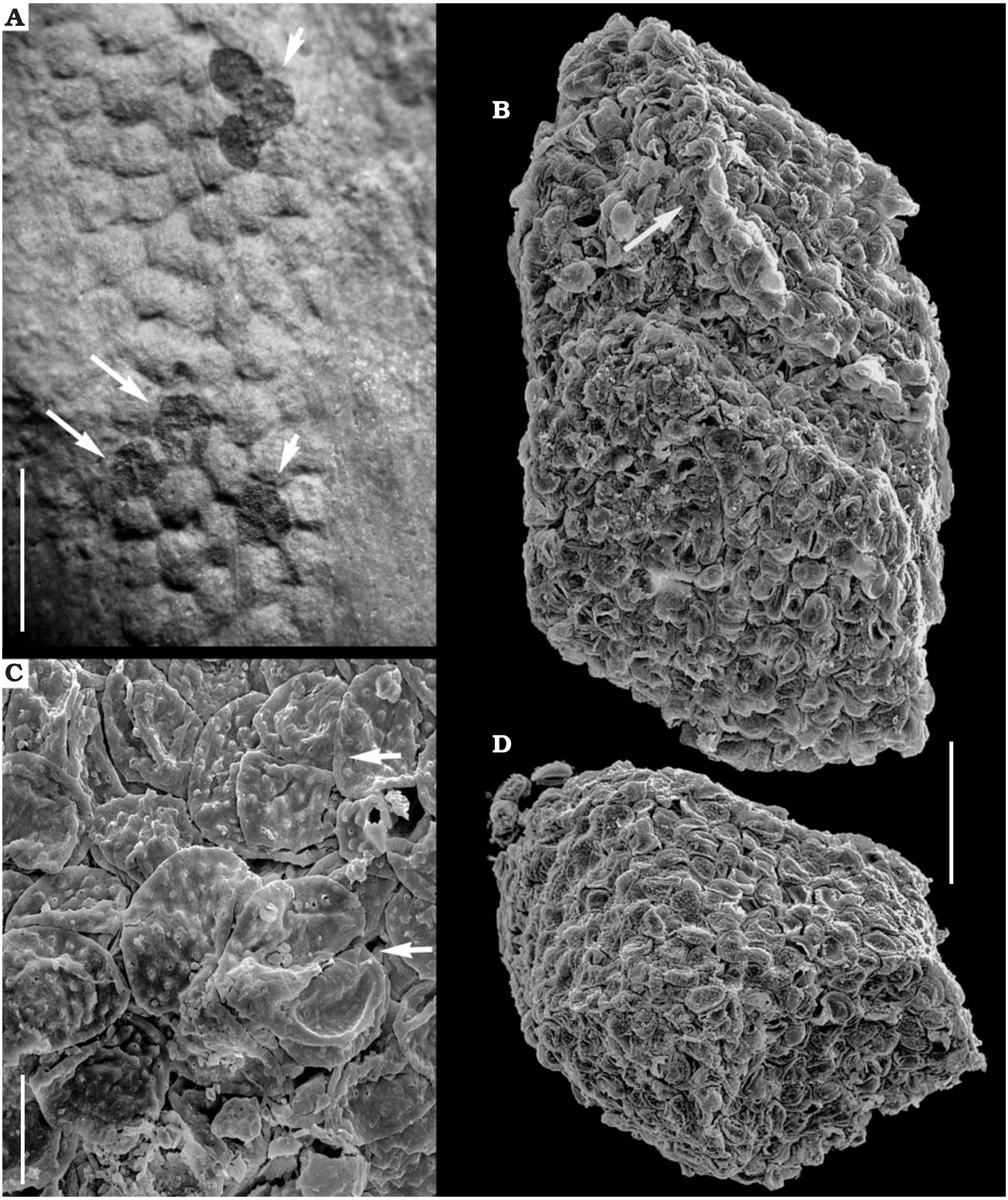

Fig. 3. In situ masses of microspores of isoetalean microsporophyll (MPZ 2010/919) from Estercuel locality, latest Albian. **A.** Detail of the microsporangium with six masses of microspores, some of them showing a false "trilete" mark (arrows) probably due to a post-sedimentary compression process. **B**, **D**. Masses of hundreds of microspores, the false "trilete" mark due to compaction within adjacent polygonal bodies inside microsporophyll (arrow). **C**. Detail of microspores presumably grouped in tetrads (arrows) showing both proximal and distal faces. B–D, SEM micrographs. Scale bars: A, 5 mm; B, D, 100 µm; C, 20 µm.

to punctate, however it seems from the photographs that the proximal face is verrucate and distal face baculate (Grauvogel-Stamm and Duringer 1983: pl. 6), similar to herein described microspores. Moreover, in situ microspores of *Isoetites brandneri* from the Triassic of the Dolomites (northern Italy) could belong to the genus *Aratrisporites* (Kustatscher et al. 2010: pl. 2: 4), however, proximal and distal sculptures of those microspores are not described and they are difficult to observe from the figure. It seems that in *Aratrisporites flexibilis* and *A. paenulatus* Playford and Dettman, 1965 the proximal face is verrucate and the distal face baculate.

According to Playford and Dettmann (1965) *Peromonolites* Couper, 1953 differs from *Aratrisporites* in having a sculptured inner wall layer. Brenner (1963) described the species *Peromonolites allensis* as having a smooth inner layer and an extremely wrinkled outer layer. However, this character is very difficult to observe, and hence it is not very useful for systematics. There are also some problematic species included in the genus *Peromonolites* such as *Peromonolites archangelskii* Baldoni, 1987, which lacks a cavate exine (Baldoni 1987) and *Peromonolites problematicus* Couper, 1953, which lacks an evident aperture and has morphological similarities to the trilete *Bryosporis anisopolaris* Mildenhall, 1990 (Bussell and Mildenhall 1990). For this reason, a more detailed taxonomic revision of the genera *Aratrisporites* and *Peromonolites* seems necessary, in order to better understand those morphotypes. Thus, we have used the first described genus *Peromonolites* Couper, 1953, which also coincides with the terminology used for Cretaceous–Cenozoic spores.

Microspores studied herein resemble more closely *Peromonolites densus* Harris, 1965 characterized by a thick perispore and granulate ornamentation with granules which are more or less uniformly distributed. The presently described in situ microspores are very different from *Peromonolites archangelskii* Baldoni, 1987 which are not cavate spores and present a fibrous ornamentation on both faces so this species should not be included within this genus. *Peromonolites asplenoides* Couper, 1958 differs by a greater size (overall 70–90 μm) and thicker perispore (about 25 μm in thickness). *Peromonolites bowenii* Couper, 1953 differs in having a verrucate ornamentation on both faces. *Peromonolites granulatu*s Norton, 1969 is distinct in having a baculate to granulate ornamentation and indistinct laesura. *Peromonolites pehuenche* Volkheimer, 1972 differs by its distinct irregularly-shaped hyaline perispore, a more circular outline of the spore and microgranulate ornamentation. *Peromonolites subengelmannii* (Elsik, 1968) Jameossanaie, 1987 differs in having a less distinct laesura, thicker perine and microgranulate ornamentation on both faces. *Peromonolites vellosus* Partridge in Stover and Partridge, 1973 is distinguishable from microspores studied herein by having a thicker perispore and fibrous, mat-like ornamentation on both faces. *Peromonolites fragilis* Burger, 1966, without any indication of tubercles in the original description, differs in having a minutely and densely wrinkled, scabrate-reticulate ornamentation on both faces, with the perine more loosely attached. *Peromonolites allensis* Brenner, 1963 is distinct by its highly wrinkled perine which is more closely attached to the central body, and a smaller camera.

The microspores are typically tuberculate similar to the modern species *Isoetes capensis* Duthie, 1929 from South Africa (Tryon and Lugardon 1990: 624, fig. 232.14), which also shows a circular aperture at the end of the tubercles.

Discussion

Microspore masses and their development.—The morphological variability of spores inside sporangia is related to their stage of maturity. Developmental series ranging from circular inaperturate to triangular trilete spores, have previously been noticed for the matoniaceous fern *Weichselia reticulata* from the Escucha Formation of north-eastern Spain (Diez et al. 2005). However, in the present study, all microspores inside the masses show similar morphologies apparently grouped in tetrads (Fig. 3C), morphologically equivalent to dispersed microspores in the same stratigraphic level (Fig. 4F, G). This is an important feature as in situ fossil isoetalean microspore tetrads have only been found in the Carboniferous cormose lycopod *Chaloneria*, as the trilete microspore type *Endosporites* (Pigg and Rothwell 1983; Pigg 1992). The similar morphology in both in situ and dispersed microspores suggests that the microspores were mature before dispersal, as they appear without separation from one another. The microspores are closely compressed forming a spherical mass and they seem to be imbricated without any indication of any organic cementation or any structure of attachment. The presence of such grouping in the studied material differs from the microspores of the living genus *Isoetes* that detach directly from the sporangia. In isoetalean lycopsid *Lycostrobus scottii*, the in situ microspores from pleuromeian cones occur in spherical groups (Pigg 1992), and it has been suggested that the grouping may have been the result of sporangial trabeculae (partitions) that were not preserved (Nathorst 1908; Taylor et al. 2009). Similarly, there is a strong possibility that this Cretaceous *Isoetites* may have had sporangia which were divided by trabeculae into a simple polygonal arrangement forming a reticulum. The upper leaves (microphylls or sporophylls) of the modern isoetalean lycopsids and the specimen studied herein, have a series of regularly spaced trabeculae, which are arranged transversely to the axis of the leaf. In modern isoetalean sporangia, trabeculae develop as parallel sheets that cross the sporangium. The breakdown of the parenchyma and tapetum during maturity or fossilisation would clearly lead to the production of polygonal spore masses. However, the confirmation of this hypothesis needs better preserved specimens. This configuration favors the concentration of microspores in masses, having a similar shape and size as megaspores. The situation in living *Isoetes* might be a vestigial trace of

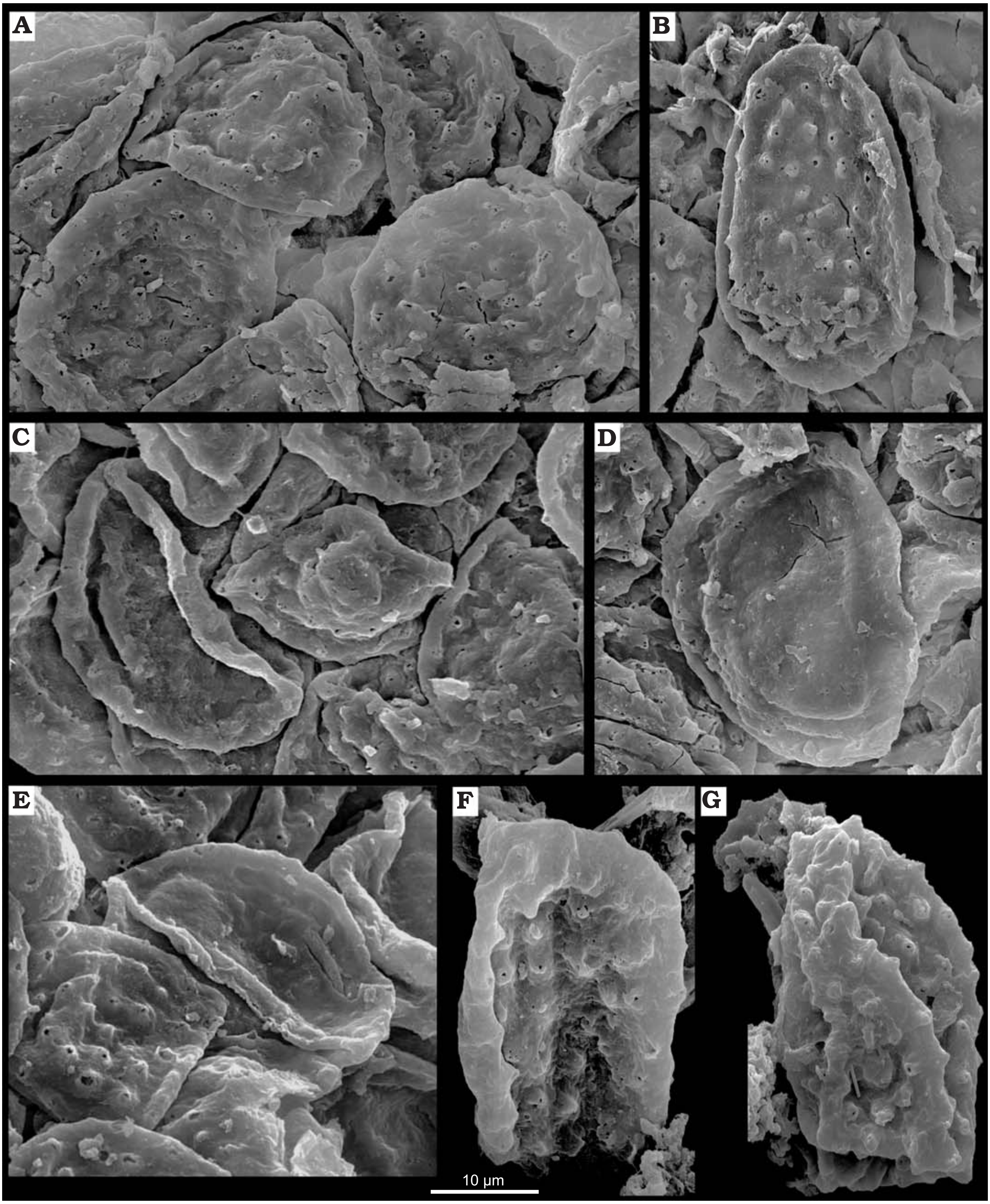

Fig. 4. **A**–**E**. SEM micrographs of isoetalean masses from *Isoetites* sp. (MPZ 2010/919) from the uppermost Albian of northeastern Spain. In situ microspores showing distal face (**A**), distal face with characteristic tuberculate ornamentation (**B**), and proximal face with the laesura extending the whole length of the grain and psilate ornamentation (**C**–**E**). **F**, **G**. Dispersed isoetalean microspores of the genus *Peromonolites* from Estercuel deposits similar to herein described in situ ones.

this system but there is no need for *Isoetes* to be the same as a Cretaceous form.

There are some evidences indicating that there is a single microsporangium with a reticulate structure and that multiple sporangia are not involved. The reticulate microsporangium shows polygonal structures of different shapes (Fig. 3A, B, D). They are predominantly polygonal bodies, being hexagonal, pentagonal and even trapezoidal. The structures have different shapes, besides, they have variable sizes (Fig. 3A, indicated by white arrows). Those two features are not consistent with the development of multiple sporangia observed in different groups of plants that present these structures (including lycophytes). The individual microsporangia of those groups have regular shapes and sizes, very similar one another (see examples in Taylor et al. 2009). If multiple sporangia were involved, as in some types of lycophytes (Taylor et al. 2009), individual microsporangia should be attached around a hypothetical axis, however, no fixing structures (stalk or pedicel) of possible microsporangia have been noticed.

The significance of microspore masses for microspore dispersal.—Two different dispersal mechanisms have been described for isoetalean spores: (i) they appear in spore masses for Jurassic megaspores (Banerji 1989; Marcinkiewicz 1989) and Triassic microspores (Nathorst 1908), (ii) microspores appear attached to megaspore sculptural elements for Cretaceous and younger isoetaleans (Batten 1969; Musselman 2002). Monolete microspores similar to those of living *Isoetes* have been previously reported adherent to the surface sculpture of isoetalean megaspores: entangled in the capilli of *Paxillitriletes vittatus* Kovach and Dilcher, 1985 from the Cenomanian of Kansas (Kovach and Dilcher 1985), of *Paxillitriletes alatus* from the late Santonian of Georgia (Lupia 2011), of *Paxillitriletes fairlightensis* (Batten, 1969) Hall and Nicolson, 1973 and of *Dijkstraisporites helios* (Dijkstra, 1951) Potonié, 1956 from the Barremian of Brilon-Nehden in Germany (Wilde and Helmsley 2000). Those monolete microspores adherent to *Paxillitriletes fairlightensis*, *P. vittatus* and *Dijkstraisporites helios* appear similar to those compared to *Perinomonoletes* Krutzsch, 1967 (Kovach and Dilcher 1985; Wilde and Hemsley 2000).

The presence of masses could represent a primitive strategy of spore dispersal and an important aspect of the early evolutionary history of this genus, as there is no any modern analogous isoetalean species showing this kind of maturation of microspores. Oval grouping of in situ megaspores have been reported from Jurassic deltaic deposits in India (Banerji 1989), however, this author does not specify any information about the disposition of in situ microspores. However, the grouping of microspores in masses may be related to dispersal mechanism. The likely mechanisms for microspore mass dispersal are zoochoric and hydrochoric dispersals.

The benefits of this microspore grouping may be that megaspores and microspore masses could be transported far away adhered to an animal (shellfish, fish, reptile or other) or by ingestion, and easily colonize new areas by large number of microspores. Contrary, there is a mechanism of dispersion in modern isoetalean plants enabling the transport of megaspores and microspores of the same Isoetes plant together. This transport would be favoured by water currents as isoetalean plants have an aquatic, or seasonally amphibious habit. Musselman (2002) indicates a possible method for microspore dispersal of *Isoetes*, in which microspores become trapped within the cavities of the surface of megaspores, being transported together by subaqueous flow. Cretaceous *Minerisporites* with microspores attached to their bodies have been reported and illustrated previously, often in the cavities of the reticulum of the megaspore (Collinson et al. 1985; Collinson 1991; Batten and Collinson 2001). They may adhere by other means, as noted in part of the studies of microspores adhering to *Molaspora* (David J. Batten, personal communication 2012). For microspore masses described here, the dispersal mechanism by a subaqueous stream would be advantageous. It could represent a more effective dispersal syndrome, as spore masses may settle quicker to bottom of water than individual microspores, showing a similar hydrodynamic behaviour to megaspores, since both have very similar morphologies and sizes. Thus, the two types of spores would be transported and deposited together in the same areas and, when conditions would become favorable, fertilization may occur.

Nowadays this type of dispersion within isoetaleans is unfavourable possibly related to ecological and/or environmental changes. It is known that in aquatic environments, water depth and current velocities affect the way of reproduction of several plant species (Haslam 1978). This new form of dispersion may be most advantageous in flooding events and subsequent habitat recolonization over other groups of plants, which would result in a better adaptation to stressful conditions. The development of spore masses may be also beneficial in tidally-influenced environments with turbulent water flows. They may, together with megaspores, settle nearest to the source than individual microspores and they would have higher change for more effective reproduction. Hence macro- and microspores may stay together affiliating the fertilization process.

Conclusions

This study presents the in situ microsporophyll associated with fossil isoetalean remains (leaf, microsporangia, and microspores) from the uppermost Early Cretaceous of north-eastern Spain. The microsporophyll is characterized by having trabeculae in the lamina, an expanded base with the impression of a ligule, and an elongate microsporangium. It is assigned to the genus *Isoetites*. This is the first description of Mesozoic isoetalean microsporophyll with many in situ masses containing hundreds of microspores. The clustering of microspore tetrads, and the fact that the spore masses are present outside the sporangium, dispersed onto the leaf lamina, is a distinct new feature that is interpreted as a different type of spore dispersal, with no modern isoetalean analogue. The in situ microspores are more closely related to *Peromonolites densus* showing a botanical affinity to the modern genus *Isoetes*. The fact that all microspores, apparently still in tetrads, of *Peromonolites* present the same stage of maturity within the spore mass, similar to those of dispersed spores, indicate that spores develop before being released in masses from the megasporangium.

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