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## Review of Palaeobotany and Palynology

journal homepage: [www.elsevier.com/locate/revpalbo](http://www.elsevier.com/locate/revpalbo)Biogeographic implications of Albian *Mohria*-like spores (Family Anemiaceae) in SW Gondwana (Patagonia)

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## ABSTRACT

The schizaeacean extant genus *Mohria* has a distribution restricted to South Africa and Madagascar area. Its cicatricose spores are characterised by their large size and muri with hollow longitudinal channels unknown in other schizaeacean genera. Fossil spores that sometimes have been referred to *Mohria* lack this typical character and therefore the determinations were discarded. Early Cretaceous (Albian) sediments from Patagonia, referred to the Piedra Clavada Formation of the Austral Basin, contain spores that have the characters now found in *Mohria*. These fossils are hereby assigned to the new genus *Palaeomohria* that includes several morphological types. The paleogeographical proximity of South Africa and Patagonia in Southwestern Gondwana persisted from the Permian to the Early Cretaceous, during a time when floras of both regions had significant similarities. In this context, the finding of *Mohria*-like spores in Patagonia suggests that the distribution of this fern was more extended in the past and became restricted while the continents shifted apart during the Cretaceous/Tertiary. The two living *Mohria* species may then represent relict taxa of a much more varied and rich group that flourished during the Early Cretaceous in SW Gondwana.

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## 1. Introduction

The fern family Anemiaceae is currently represented by two genera: *Anemia* Swartz and *Mohria* Swartz (Smith et al., 2006). There are approximately 100 species of *Anemia* which primarily inhabit tropical or subtropical areas in the New World. *Mohria* is restricted to Madagascar, South Africa, Mozambique and the adjacent Mascarene Islands (Tryon and Lugardon, 1991). Two species are known: *Mohria caffrorum* (L.) Desv. and *M. lepigera* (Baker) Baker. Both *Mohria* and *Anemia* have typical cicatricose trilete spores that mainly differ in the structure of their muri. The muri are hollow in *Mohria* while in *Anemia* they are solid or have internal micropores (Erdtman, 1957; Mickel, 1962; Tardieu-Blot, 1966; Dettmann and Clifford, 1991; Tryon and Lugardon, 1991; van Konijnenburg-van Cittert, 1991, 1992; Dettmann and Clifford, 1992).

The typical cicatricose ornamentation facilitates identification of fossil spores related to *Anemia*, some of which have been found *in situ* in sporangia borne on pinnules of fertile fronds (Skog, 1992; Van Konijnenburg-Van Cittert, 1992; Dettmann and Clifford, 1992). This spore type prevailed worldwide during the Upper Mesozoic, particularly in the Aptian and Albian Stages. The variety of cicatricose sculptures seen in fossil palynomorphs inspired detailed studies to look for relationships with extant taxa and to explore their potential as

stratigraphic markers (Hughes and Moody-Stuart, 1967; Davies, 1985; Burden and Hills, 1989; Dettmann and Clifford, 1992, among others). At present the following genera of dispersed fossil spores are related to *Anemia*: *Cicatricosisporites* Potonié and Gelletich, *emend.* Dettmann and Clifford; *Appendicisporites* Weyland and Krieger, *Ruffordiaspora* Dettmann and Clifford; *Nodosisporites* Déak, *emend.* Dettmann and Clifford and *Plicatella* Maljavkina, *emend.* Burden and Hills (not accepted by some authors who regard it as a synonym to *Appendicisporites*).

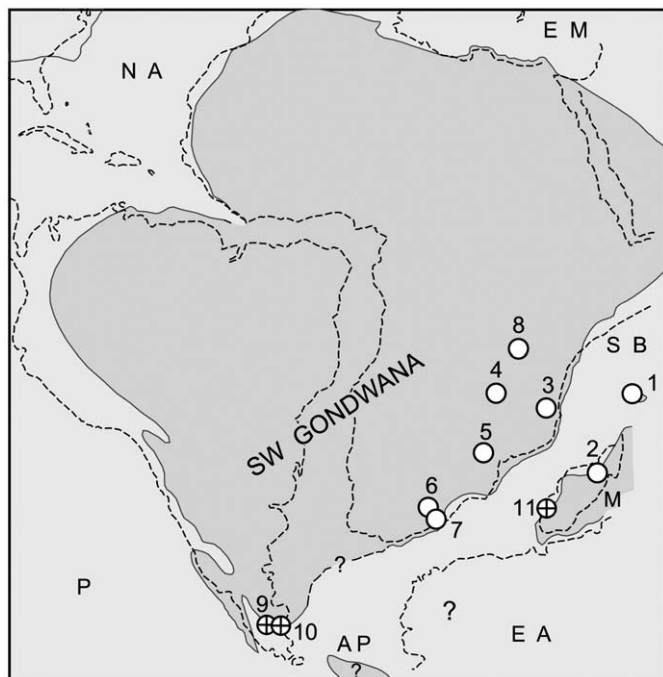
In this paper, cicatricose spores having hollow ridges (muri) are described from several Early Cretaceous sites of Southern Patagonia. The muri suggest that these spores are related to *Mohria*, a genus presently restricted to South Africa. The paleogeographic unity of South Africa and South America goes back to the Late Palaeozoic (Pankhurst et al., 2006), and the separation of the two continents commenced in the Late Jurassic/Early Cretaceous. This slow shifting apart must have played a role in the progressive differentiation of floras from both regions. *Mohria* is presently absent in South America, while during the Early Cretaceous *Mohria*-like ferns occupied both geographic regions as suggested by palynological and putative palaeobotanical data.

## 2. Materials and methods

All Patagonian specimens were found in the Piedra Clavada Formation. They were recovered at the type section (at the homonymous locality, Archangelsky et al., 2008) and north of the Lago Cardiel at the Cerro Bayo section, Santa Cruz province, Southern

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**Fig. 1.** West Gondwana during the Aptian/Albian (plain gray). Dashed lines outline present day Africa, Madagascar and South America. Exact placement of the Antarctic Peninsula (AP) and Eastern Antarctica (EA) remains uncertain. (Modified from Owen and Mutterlose, 2006). NA = North Atlantic; EM = Eastern Mediterranean; SB = Sudan Basin; M = Madagascar; P = Paleopacific Ocean. Extent of Southern Atlantic between Africa and South America remains uncertain. Open circles represent localities where living *Mohria* species are found: 1 = Mascarene Islands; 2 = Madagascar; 3 = Mozambique; 4 = Zambezie River/Zambia/Malawi/Nyassa; 5 = Zimbabwe; 6/7 = S.E. Africa (Natal,Kvazulu); 8 = Tanganika/Tanzania. Circles crossed inside represent sites where putative *Mohria*-like fossils occur: 9/10 = Patagonia (*Palaeomohria* spores; 11 = Madagascar) (fertile *Mohriopsis* fronds with sporangia).

Patagonia (Fig. 1). This unit bears ammonites and is dated in the Early-mid Albian (Aguirre Urreta, 2002; Medina et al., 2008). The type section yielded two levels with pollen (PTL 44/03 and PTL 46/03, Archangelsky et al., 2008) while the Cerro Bayo section yielded *Mohria*-like spores from three levels (1/01, 2/01 and 3/01) (Ramos, 1984; Villar de Seoane and Archangelsky 2008).

The samples were treated with the usual technique: HCl to remove carbonates, HF to remove silicates, washing and sieving through 10- $\mu$ m, 25- $\mu$ m and 37- $\mu$ m meshes and mounting in glycerine jelly with phormol to make permanent slides (Gamerro and Cárdenas, 1980). For SEM observation, the residue was mounted in stubs and coated with gold and palladium. A Zeiss Axioscope was used for observation and a Nikon Coolpix 950 for photography. A Phillips XL30 TMP of the Buenos Aires Nat. History Museum was used for SEM observation and photography. England Finder coordinates of illustrated specimens are mentioned in the figure legends.

All slides are lodged in the paleopalynological collection of the Buenos Aires Nat. Hist. Museum (BA Pal.) while MEB stubs are stored in the Paleobotanical Collection of the Museum (BA Pb MEB).

### 3. Systematic descriptions

#### Family Anemiaceae Link 1841

The recent classification of extant ferns by Smith et al. (2006) is followed here. The Anemiaceae, together with the Schizaeaceae (genera *Actinostachys* and *Schizaea*) and Lygodiaceae (genus *Lygodium*) are included in the Order Schizaeales. The Anemiaceae include the genera *Anemia* and *Mohria*, which are considered to be closely related in the same clade.

#### 3.1. Comments on the genus *Mohria*

The genus *Mohria* Sw. is presently exclusive to Southern Africa and adjacent Madagascar (Fig. 1). Together with *Anemia* both are included in the family Anemiaceae to underscore their close relationship (Nayar and Kaur, 1971; Smith et al., 2006; Schuettpelz and Pryer, 2007). However, there are differences between the genera: (1) the stems of *Anemia* (and the other schizaeaceous genera), are covered by hairs, while in *Mohria* they have scales instead (Mickel, 1962; De la Sota and Morbelli, 1987). (2) Both have stems with dictyostele but *Mohria* lacks axillary pockets (Mickel, 1962); stomata in *Anemia* are of a peculiar type called “floating stomata”, a condition termed “adetostomy” (Mickel and Lersten, 1967; Wikström et al., 2002), and this condition does not occur in *Mohria*. (3) In the schizaeoids the leaf surface has hairs or is glabrous, while in *Mohria* it has scales, a character that was used to segregate the genus in a distinct family, Mohriaceae (Reed, 1947). (4) *Anemia* fronds are dimorphic (except in *Anemia colimensis*, which has monomorphic fronds but only the basal pinnae are fertile: De la Sota and Morbelli, 1987; Wikström et al., 2002), while fronds are monomorphic in both *Mohria* species, a condition that was interpreted as primitive (Copeland, 1947). (5) Sporangia are ovate-globose in *Anemia* while globose (spherical *ap.* Skog, 1992) in *Mohria*. Finally, (6) the spores in *Mohria* are large (88–110  $\mu$ m), with a single longitudinal channel in each ridge, while in *Anemia* they are usually smaller and ridges are solid or porous.

The number of spores reaches 256 per sporangium in both genera (De la Sota and Morbelli, 1987) and they share the basic chromosome number ( $x = 19$ , Löve et al., 1977).

The hollow, longitudinal internal channel located in the centre of each ridge is typical to *Mohria*, a character stressed by Erdtman (1957, Fig. 143J) and Erdtman and Sorsa (1971:126) when they mention that, “In the basal part of the muri is a channel, about 1.0  $\mu$ m high and less than 0.5  $\mu$ m broad.” Later, this channel was mentioned and/or illustrated by several authors (Kremp and Kawasaki, 1972; Tryon and Lugardon, 1991; Van Konijnenburg-Van Cittert, 1992, among others). Mickel (1962, 1981) and Hill (1977) argued that some *Anemia* species (included in the subgenera *Coptophyllum* and *Anemiorhiza*) had hollow ridges, but Dettmann and Clifford (1991, Figs. 70–75) discarded this conclusion, showing those muri to have microporate structure rather than a hollow single channel.

Spores having muri with a central hollow longitudinal channel have been found in several horizons from two localities in Patagonia, both attributed to the Piedra Clavada Formation of Albian age (Fig. 1). They are here referred to a new genus of dispersed spores that closely resemble the spores of the living *Mohria*.

#### 3.2. *Palaeomohria* nov. gen.

*Type species: Palaeomohria patagonica* nov. sp.

*Etymology:* The name suggests the affinity of this fossil spore type to the extant fern *Mohria*.

*Diagnosis:*

Trilete spores, equatorial outline subtriangular with concave sides and broadly rounded angles. Lips present on laesurae. Sculpture typically cicatricose, rarely canaliculate. Muri straight to weakly sinuous, parallel, forked or simple, of two types: wide (dominant) and narrow, short (rare), converging at angles where short radial ducts and protuberances may occur. Muri smooth or ornamented with verrucae. A typical inner longitudinal hollow channel is present in all muri. Perispore delicate, smooth or finely striated. Sporoderm excepting muri very thin.

*Comments.* The oldest putative member similar to *Mohria* was described from the Upper Jurassic of Madagascar as *Mohriopsis plastica* (Appert, 1973). It was based on sterile and fertile fronds, although no spores were found inside the sporangia. This fossil was also considered to be similar to the schizaeaceous *Klukia* or *Stachypteris*

(Van Konijnenburg-Van Cittert, 1992), and at present there is no consensus that it is in fact related to *Mohria* (Dettmann and Clifford, 1992).

No confident records of fossil spores with *Mohria* type sculpture (hollow ridges) have been reported (Dettmann and Clifford, 1992). However, it should be noted that this character could have been overlooked in taxonomic descriptions of cicatricose spores. Some illustrations suggest the presence of an inner channel, e.g., Lower Cretaceous material from the Nubian Desert in Egypt that was described as *Cicatricosisporites mohrioides* Delcourt and Sprumont (Saad and Ghazaly, 1976, Pl. VI Figs. 1–2) or *C. crassiterminatus* Hedlund (Saad and Ghazaly, 1976, Pl. VI Fig. 3) and eventually might expand the distribution of *Mohria*-like spores to other regions. Fossil spores in dispersed states have been referred to *Mohria* (Bolkhovitina, 1953) and later placed in the genus *Pelletieria* (Bolkhovitina, 1961), now *Pelletixia* (Watson and Hill, 1982). However, descriptions and illustrations don't mention or show the typical hollow ridges. Moreover, *Pelletixia* was based on megafossils (Seward, 1913) bearing cicatricose spores that later were described (but not illustrated) by Couper (1958) who referred them to *Cicatricosisporites dorogensis*, the type species of the genus. Later, Davies (1985) included all fossil *Mohria* and *Pelletixia* (= *Pelletieria*) species in *Cicatricosisporites*. Other references of fossil *Mohria* spores are now referred mostly to *Cicatricosisporites* and none of them shows or mentions the typical hollow ridges.

Specimens of *Palaeomohria* are not abundant and they are restricted to two localities where the Piedra Clavada Formation is found. Most specimens are referred to the type species, *P. patagonica*, while a few others are separated as unnamed species and types. They underscore the variability of the sculpture that members of *Palaeomohria* attained during the Early Cretaceous.

The Patagonian fossils represent the first record of cicatricose spores having the characteristic hollow longitudinal channels present in all muri, a unique character among extant and fossil Schizaeaceae. This is also the first and possibly oldest reliable evidence of a putative *Mohria*-like plant from Cretaceous strata in Gondwana. Another common character to the five types studied here is their typically large size, with the equatorial diameter generally between 80 and 90  $\mu\text{m}$  and reaching 105  $\mu\text{m}$ , similar to the size found in recent *Mohria* spores that range from 67  $\mu\text{m}$  to 120  $\mu\text{m}$  (Tryon and Lugardon, 1991).

*Palaeomohria patagonica* nov. sp.

Figs. 2(3–5,8) and 3(1,3–9)

*Holotype*: slide BA Pal 5697, illustrated on Fig. 2(3–5)

*Paratype*: slide BA Pal 5697, illustrated on Fig. 2(8)

*Repository*: Museo Argentino de Cs. Ns. 'B. Rivadavia', Division Paleobotany.

*Type locality*: Lago Cardiel, Cerro Bayo Section, Santa Cruz province, Argentina.

*Stratigraphic horizon*: Piedra Clavada Formation, Albian.

*Etymology*: The specific epithet refers to its distribution in Patagonia.

*Additional material*: BA Pal 5644, 5664, 5699, BA Pb MEB 315 (Lago Cardiel, Cerro Bayo Section, levels 1/01, 2/01 and 3/01; Piedra Clavada Formation); BA Pal 6052, 6061, BA Pb MEB 263 (Tres Lagos Section, type area, levels 44/03, 46/03; Piedra Clavada Formation).

*Diagnosis*:

Equatorial contour subtriangular of convex sides and broadly rounded angles. Laesurae slightly sinuous, with short lips, reaching half of the spore radius. Sculpture cicatricose, muri 3.3–6.8  $\mu\text{m}$  wide and 1.6–2.8  $\mu\text{m}$  high, straight to slightly sinuous, simple or bifurcated, with a clear medial internal and longitudinal hollow channel. Luminae 1.6–4.5  $\mu\text{m}$  wide. Set of 4 muri and 4 luminae 18.3–30.7  $\mu\text{m}$  wide. Short and thinner muri, 1.2–1.7  $\mu\text{m}$  wide, may be present between main, thicker ridges. Four to 6 proximal and distal muri, parallel or slightly oblique to the equator, are arranged in three series that coalesce at angles, where few irregular and strong verrucae 1.2–7.3  $\mu\text{m}$  wide and 2.7  $\mu\text{m}$  high occur. Dispersed verrucae are occasionally

found in luminae. The exine is smooth and delicate, 0.3–0.7  $\mu\text{m}$  thick, excepting muri. Perispore present.

*Size*: Equatorial diameter, 60–95  $\mu\text{m}$  (22 specimens).

*Description*: The spores in polar view have a subtriangular equatorial contour with broadly rounded angles and slightly convex sides (Figs. 2(3); 3(3,4)). The laesurae are slightly sinuous and extend for half the equatorial radius, bearing inconspicuous short lips, up to 3  $\mu\text{m}$  high at pole. A highly reduced contact area is seen in some specimens (Fig. 3(3,4)). The exine sculpture is mainly cicatricose with straight to slightly sinuous muri, showing by transparency a medial longitudinal hollow channel over which the mural roof often is depressed or has collapsed (Figs. 2(8); 3(4–6)). It was also seen in cross sections of muri (Fig. 3(9)). This single inner channel found in all muri extends along their entire length. The width of muri is usually equal to or slightly wider than neighbouring lacunae; however, some specimens show occasional larger valeculae (Figs. 2(4,8); 3(5)). Individual muri may occasionally bifurcate and anastomose with neighbouring muri (Figs. 2(4); 3(8)). Short, thin muri located between normal muri are also found, especially in equatorial areas (Fig. 3(4,6)). Three series of four to six muri, subparallel or slightly oblique to the equator, are located at both proximal and distal sides of the spore. Muri at the proximal side of the spore coalesce at angles where a tuberosely thickened area of variable size is developed (Figs. 2(4); 3(3,4)). A few conspicuous verrucae occur near or in this thickened area.

Occasional verrucae are also found randomly in the inter-radial area of the spore. Sometimes, at the distal pole a triangle is formed by coalescent muri, with a few isolated short muri or ridges inside (Fig. 2(8)), closely similar to that illustrated in the living species *Mohria caffrorum* (Van Konijnenburg-Van Cittert, 1992, Pl. 1 Fig. 8). On the distal side muri are laterally continuous while crossing the radial areas, where they may expand slightly. Individual muri are 3.3–6.8  $\mu\text{m}$  wide to 1.6–2.8  $\mu\text{m}$  high, have rounded crests and are separated by luminae 1.6–4.5  $\mu\text{m}$  wide. The total width of 4 muri and 4 luminae is 18.3–30.7  $\mu\text{m}$ . Except for the muri, the exine is delicate, 0.3–0.7  $\mu\text{m}$  thick and looks almost transparent. This causes an irregular, wavy arrangement of muri in specimens in which the exine of the lacunae has almost collapsed. Some specimens (Fig. 2(3,4)) on the proximal face may show short and close muri partially occupying the small contact area up to the laesura and oblique to the normal sets of long parallel muri. In this case, luminae are much narrower than in typical specimens of *P. patagonica*. Thin, delicate wrinkles are perpendicularly placed to muri; they probably represent remnants of a perispore (Fig. 3(7,8)).

*Comments and comparisons*: Due to the delicate nature of the exine some specimens appear distorted and the disposition of muri sets may vary significantly in different compression planes. In these cases, their separation is more pronounced than in better-preserved material.

The hollow *Palaeomohria* muri converge toward the spore angles where specialised structures develop as short, radially extended ducts surrounded by verrucae (Fig. 3(5,6)). It is possible that these structures and the hollow mural channels were involved with controlling liquid flow to help germination and/or spore dispersal.

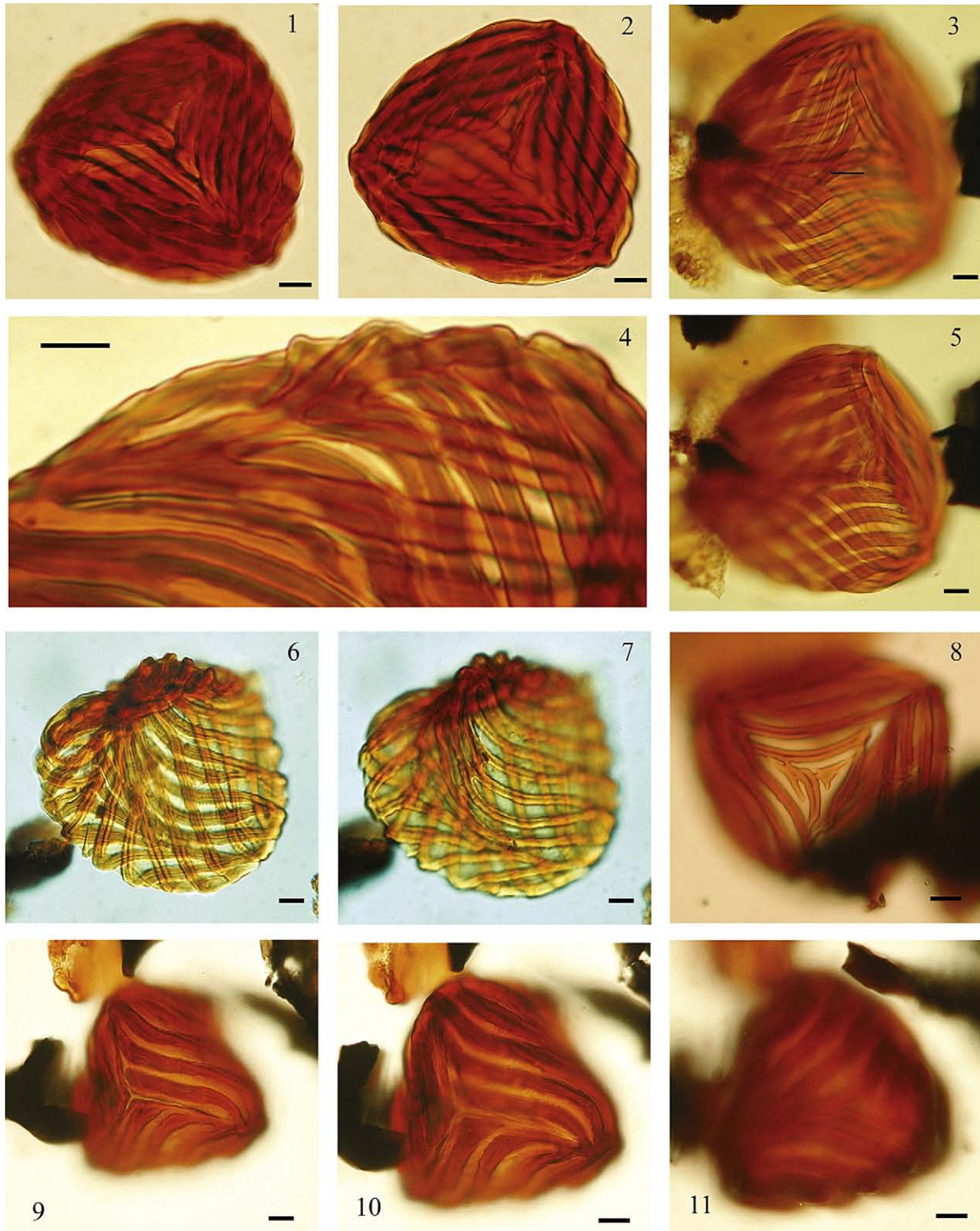
Both living *Mohria* species have an equatorial diameter of 67–120  $\mu\text{m}$ , and their muri are wider than adjacent luminae. The arrangement of muri is similar to the *Palaeomohria* species, and the central hollow channel is clearly seen by transparency as well.

*Palaeomohria* sp. 1

Fig. 2(6,7)

*Description*: Proximal side of spore not seen in the few specimens studied. They are compressed in a distal/equatorial plane and show a subcircular contour, canaliculate sculpture and widely separated muri (luminae wider than murus width). Muri may bifurcate or anastomose and possess a clear central hollow channel (Fig. 2(6)). Sides of muri irregular, undulated with a rounded top. Muri are 3–4  $\mu\text{m}$  wide while luminae are 4–7  $\mu\text{m}$  wide. Sets of 4 muri and 4 luminae are 30–40  $\mu\text{m}$  wide. Three sets of apparently 5 to 7 muri meet at angles of the

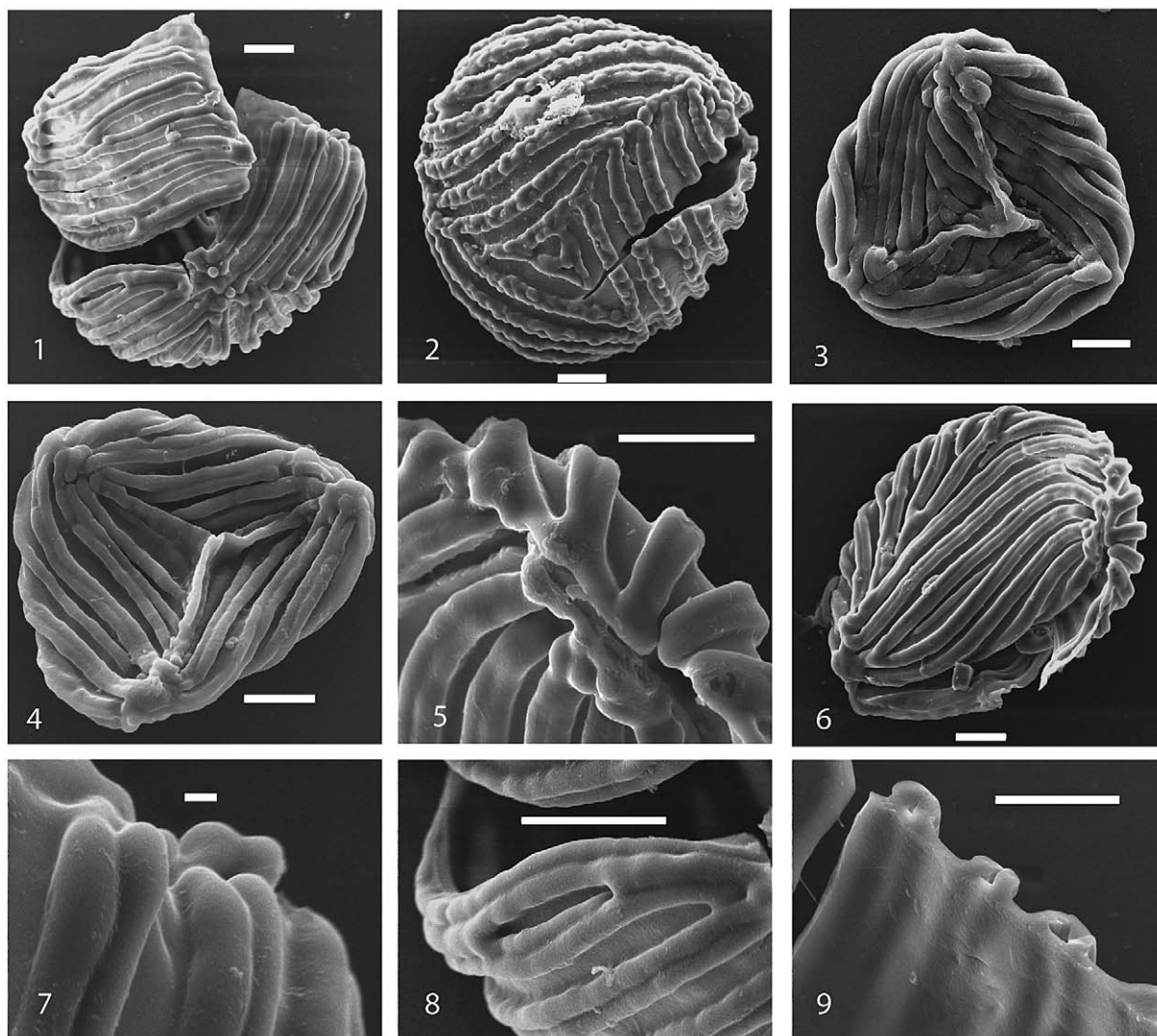




**Fig. 2.** Panels 1–2, *Palaeomohria* Type 1. BA Pal 6052, F 33/3; 1, distal focus showing closely placed muri at pole with inner longitudinal channels; 2, proximal focus showing short trilete mark and the arrangement of muri; panels 3–5,8, *Palaeomohria patagonica* nov. sp. 3–5, Holotype, BA Pal 5697, L 23/2; 3, focus on distal face showing arrangement of muri and inner longitudinal channels by transparency; 4, detail of spore angle showing irregular verrucae on muri and translucent inner longitudinal mural channels (scale bar, 4  $\mu$ m); 5, focus on proximal face partly showing delicate trilete mark; 8, Paratype, BA Pal 5697, L/31; distal face showing polar triangular area; note a translucent proximal triangle that corresponds to the detached contact area. Panels 6–7, *Palaeomohria* sp. 1. BA Pal 5697, Q 28/2. Two different foci of the spore in lateral/oblique view showing wide luminiae separating muri, the inner single longitudinal mural channels and verrucate sculpture at angle (upper part of picture). Panels 9–11, *Palaeomohria* Type 2. BA Pal. 6052, N 34/1–2; 9, focus on proximal half showing trilete mark and closely adjacent muri with medial longitudinal inner channels; 10, a slightly lower focus of proximal face showing the arrangement of muri; 11, focus on distal face showing the shadow of muri placed perpendicularly to muri of proximal face. Unless otherwise stated, scale bar = 10  $\mu$ m.

spore where they project slightly in the equatorial region (Fig. 2(7)). Exine, except for the muri, is delicate and 1–1.5  $\mu$ m thick. *Dimensions:* Equatorial diameter: 84–105  $\mu$ m (10 specimens).

*Studied material:* BA Pal 6052, 6061 (Tres Lagos section, levels 44/03 and 46/03, Piedra Clavada Formation). BA Pal 5698 (Cardiel Lake, Cerro Bayo section, level 1/01, Piedra Clavada Formation).



**Fig. 3.** Panels 1,3–9: *Palaeomohria patagonica* nov. sp. 1, a broken specimen showing muri with depressed longitudinal furrows corresponding to the inner channels and dispersed verrucae. BA Pb MEB 315; 3, proximal view of a specimen showing laesurae with lips and strong verrucae at angles; BA Pb MEB 281; 4, another specimen in proximal view showing laesurae and muri with longitudinal medial furrows; BA Pb MEB 276; 5, detail of specimen in panel 6 showing convergence of muri at angles and the equatorial radial channel surrounded by verrucae; 6, general view of specimen in panel 5; note at top left a few short muri interspersed between long muri and projecting from the other side; BA Pb MEB 315; 7, a detail of panel 1 showing muri and delicate transversal wrinkles corresponding to probable remnants of a perispore (scale bar, 1  $\mu$ m); 8, another detail of panel 1 showing anastomosis of muri and delicate transversal wrinkles of a probable perispore; 9, a section of a broken exine showing muri and a hollow centre that corresponds to the inner channel; BA Pb MEB 318; panel 2, *Palaeomohria* Type 3. BA Pb MEB 316; a specimen in oblique distal view showing muri with longitudinal furrows and supramural verrucate sculpture; the broken edge, at the right of figure, shows a few muri in section with a central hollow mark. Unless otherwise stated, scale bar = 10  $\mu$ m.

**Comments:** Although it was impossible to find a specimen showing the proximal face of the spore, the distal ornament has muri with a single hollow longitudinal channel characteristic of *Palaeomohria*. The main difference between *Palaeomohria* sp. 1 and the type species of the genus is the mostly canaliculate ornament of the spore. The diameter of the fossil is close to both living *Mohria* species (93–115  $\mu$ m).

### 3.3. Other putative *Palaeomohria* spore types

Three different types are included under this heading. The few specimens described have in common the characteristic hollow mural structure. On the other hand, they are separated from the type species and from *Palaeomohria* sp. 1 because they have a different sculptural pattern. Their inclusion in this study merely intends to underscore the variability of the sculpture that members of *Palaeomohria* developed already in the Early Cretaceous.

### *Palaeomohria* Type 1

Fig. 2(1,2)

**Description:** Only five specimens have been found. The spores are broadly triangular, almost of circular equatorial outline (Fig. 2(1,2)). The proximal face has a trilete mark that extends for half of the radius and has short, somewhat sinuous lips (Fig. 2(2)). The sculpture on both faces is cicatricose with muri much wider than the adjacent luminae. Three sets of four muri are subparallel to the equator. They pass obliquely to the distal face and coalesce at the distal pole (Fig. 2(1)). Individual muri are 3.6–4.3  $\mu$ m thick while adjacent luminae are 0.2–0.7  $\mu$ m wide. The set of 4 muri and 4 luminae is 16–17  $\mu$ m wide. Muri have a rounded top and slightly irregular sides. The middle single channel is present in all muri. The exine, excepting muri, is 0.7–1.2  $\mu$ m thick.

**Dimensions:** Equatorial diameter 60–101  $\mu$ m (5 specimens).

**Studied material:** BA Pal 6052, 6061 (Tres Lagos section, levels 44/03 and 46/03, Piedra Clavada Formation).



**Comments and comparisons:** *Palaeomohria* Type 1 is exclusive to one locality (Tres Lagos Section) and is found in two fossiliferous levels of the Piedra Clavada Formation. It is distinguished from *Palaeomohria patagonica* in the smaller equatorial diameter and the much wider muri than adjacent luminae. *Palaeomohria* sp. 1 is larger than *Palaeomohria* Type 1 and the ornamentation is basically canaliculate. The close arrangement of muri in *Palaeomohria* Type 1 provides a dense, compact appearance to this spore, quite different from the other species studied here.

#### *Palaeomohria* Type 2

Fig. 2(9–11)

**Description:** Only four specimens of this species have been found in one locality. They are well preserved and show characters that allow their differentiation from the other *Palaeomohria* species described here. The spore has a triangular equatorial outline with rounded angles (Fig. 2(9)). The laesurae extend close to the equator and are straight to slightly sinuous with short, delicate lips (Fig. 2(9)). The ornamentation is cicatricose with three sets of four strong muri that run almost parallel to the rays of laesurae and cross the equator obliquely, extending to the distal polar area where they coalesce (Fig. 2(11)). Some muri anastomose at angles (Fig. 2(10)). Width of 4 muri and 4 luminae is 29.2  $\mu\text{m}$ . Muri are 4.7–6.9  $\mu\text{m}$  wide while luminae are 2.5–3.5  $\mu\text{m}$  wide. The hollow medial channel is visible by transparency in all muri extending close to the laesurae (Fig. 2(9,10)). The delicate exine is about 1  $\mu\text{m}$  thick.

**Dimensions:** Equatorial diameter, 54–77  $\mu\text{m}$  (4 specimens).

**Studied material:** BA Pal 6052 (Tres Lagos section, level 44/03, Piedra Clavada Formation).

**Comments and comparisons:** *Palaeomohria* Type 2 differs from the other species described here in its arrangement of muri at the proximal face (almost parallel to the rays of laesurae) and in the lower number of muri in each mural set (4).

#### *Palaeomohria* Type 3

Fig. 3(2)

**Description:** Only one specimen was recovered during an SEM scan for cicatricose spores. It shows a distal face with a cicatricose/canaliculate sculpture. The equatorial contour is almost circular. Three sets of 5 to 6 parallel muri that converge in a polar triangular area are seen. The muri along their total length bear closely set conspicuous verrucae up to 3.5  $\mu\text{m}$  wide. The verrucae are arranged in two longitudinal rows separated by a depression. Isolated verrucae are also seen between muri near the angles of the spore (Fig. 3(2)). Muri are 3.4–4.2  $\mu\text{m}$  wide and 3.7  $\mu\text{m}$  high, while luminae are 3–3.7  $\mu\text{m}$  wide. A longitudinal central depression is present in some muri. It corresponds to the hollow channel that is seen in a section of the spore exine (Fig. 3(2)). The set of 4 muri and 4 luminae is 28–31  $\mu\text{m}$  wide. The exine, excepting muri, is 0.6–1  $\mu\text{m}$  wide.

**Dimensions:** Equatorial diameter 80  $\mu\text{m}$  (one specimen).

**Material studied:** BA Pb MEB 316 (Tres Lagos section, level 44/03, Piedra Clavada Formation).

**Comments and comparisons:** This single specimen is included in *Palaeomohria* because it shows the typical medial longitudinal channel inside its muri. It is easily differentiated from the other species of *Palaeomohria* described here by the conspicuous verrucose supra-mural sculpture, present also in luminae at spore angles. In this respect, this sculpture is similar to the tubercles found in both living *Mohria* species, especially in *M. caforum* (Tryon and Lugardon, 1991, Figs. 30.3 and 30.6). The large size is closely comparable with other species of *Palaeomohria*.

### 3.4. Discussion

Dettmann and Clifford (1992, Table 2) recognised 12 characters in recent and fossil striate schizaeaceous spores (including the pteridaceous genus *Ceratopteris*), and used these characters for a phylogenetic analysis relating the extant species of *Anemia* and

*Mohria* (and *Ceratopteris*) with recognised fossil genera (*Cicatricosisporites*, *Plicatella*, *Appendicisporites*, *Nodosisporites*, *Ruffordiaspora*, *Fisciniasporites* and *Magnastriatites*). The hollow muri is an exclusive character of *Mohria* that has not previously been described in fossil dispersed cicatricose spores. All references to fossil spores of this genus by different authors have been discarded because muri show no inner hollow duct (Dettmann and Clifford, 1992). However this mural structure may have been overlooked in some cases, and therefore such records should be reinvestigated in order to confirm their presence.

*Palaeomohria* has this character in all types described here. Other characters that are shared with extant *Mohria* spores are the 3 sets of muri, the distal/radial mural anastomoses and the verrucate supra-mural sculpture of *Palaeomohria* Type 3, comparable to the tuberculate sculpture present in both living *Mohria* species. The usually cicatricose sculpture that some of our types show is another shared character with *Mohria*; however, a canaliculate sculpture is also present in *Palaeomohria* sp. 1. The presence of both types of sculpture (canaliculate or cicatricose) may be considered an ancestral and generalised characteristic that differentiates the more specialised *Mohria* from *Palaeomohria*. Taking these facts into consideration it is suggested that the main character of *Mohria* spores is the hollow mural structure, as defined by Dettmann and Clifford (1991, 1992). For this reason all the Patagonian types described here are referred to the new morphogenus *Palaeomohria*, suggesting its affinity with the living genus.

The hollow channel that characterises the muri of *Mohria*, now found in fossil spores, is a conservative feature that may have a strong phylogenetic signal suggesting that the difference between solid, porous and hollow mural structures had already evolved by the mid-Cretaceous in this clade. Furthermore, this structure found in recent and fossil spores of this clade is enhanced by its probable (harmomegathic?) function to help germination and/or spore dispersal. *Palaeomohria* now extends the paleogeographic distribution of this spore type to Patagonia and invites investigation for other fossil records, especially in SW Gondwana where *Mohria* is now confined.

### 4. Paleobiogeographic aspects

The two living *Mohria* species are currently restricted to South Africa and probably represent relictual taxa of an ancient stock that during the Early Cretaceous occupied an extended area of southwestern Gondwana. This is in line with several similar Aptian and Albian fossils found in South Africa and southern South America (Archangelsky, 1967; Appert, 1973; Anderson and Anderson, 1985; Archangelsky, 1996; Zavada, 1987; Anderson et al. 1999), and the Patagonian cretaceous *Mohria*-like spores represent a further record common to both continents.

The paleogeographic history of Patagonia goes back to the Permian when the fossil floras were similar to those found in some areas of South Africa (Walton, 1929; Teixeira, 1947; Lacey and Huard-Moine, 1966; Archangelsky and Arrondo, 1975). New geochronological, gravimetric and tectonic evidence suggest that during the Permian, Patagonia was an allochthonous or parautochthonous terrane, close to the Gondwana Continent (Rapela, 1997; Pankhurst et al. 2006; Ramos 2007). The southwestern Gondwana paleofloristic realm persisted during the Triassic, and South African paleofloras remained remarkably similar to those from southern South America (Anderson et al., 1999). The Late Jurassic–Early Cretaceous paleogeography of Southwestern Gondwana shows both continents united until the break-up of Africa and South America gave birth to the Atlantic Ocean (Uliana and Biddle, 1988; Owen and Mutterlose, 2006). The few Eocretaceous megafloora and microflora studies support this paleogeographic link (Archangelsky, 1967; Scott, 1976; Anderson and Anderson, 1985; Zavada, 1987; Anderson et al., 1999, among others). The new paleogeographic scenario was established during the Aptian, including the Patagonian Austral Basin, and also a seaway which separated

Madagascar from continental Africa, and connected directly northeast with Iraq and Indian Spiti (Ballent and Whatley, 2006; Owen and Mutterlose, 2006).

*Palaeomohria* spores extend to Patagonia the range of putative *Mohria*-like ferns (Fig. 1). At the same time they confirm that this lineage was well established during the Early Cretaceous and was represented by several species. In this context, the two living species of *Mohria* may be considered relict taxa in view of their restricted geographic distribution.

## 5. Conclusions

Information is slowly accumulating about fossil *Mohria*-like spores. So far, only putative fossil remains have been referred to the genus (Appert, 1973). References to fossil *Mohria* spores have been rejected because they lacked the differentiating character of muri with a longitudinal central hollow instead of a porous or solid structure (Dettmann and Clifford, 1991, 1992). This character, unique to extant *Mohria*, has been reported for several Lower Cretaceous species found in southern South America, here included in the new genus *Palaeomohria*. Two species and three additional informal types are described demonstrating the diversity of *Mohria*-like spores extending back to the Albian. This character may have a phylogenetic significance by suggesting that the *Mohria* lineage may be traced back to the Early Cretaceous, in line with megafossils of similar age described from Madagascar (Appert, 1973). This peculiar (harmomegathic?) mural structure may have functioned to assist spore germination and/or dispersal.

The Patagonian spores also suggest that *Mohria*-like plants occupied a wide area in Southwestern Gondwana during the Early Cretaceous, when the first tectonic events initiated the break-up and shifting apart of both continents. South America was close to both Madagascar and southern Africa at the time, and no geographic barriers existed while the Atlantic Ocean was in its initial stage of development. After the separation of the continents, plant assemblages of South Africa and Patagonia began to differentiate. In this regard, *Palaeomohria* probably represents one of the last records of *Mohria*-like plants in southern South America. The poorly explored region of SW Gondwana needs more field and laboratory research as to extract new paleofloristic information on fossil plant assemblages and a better understanding of the diverging path that led to the present day vegetation on both continents.

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