Fungal fruiting bodies in the Cullen Formation (Miocene) in Tierra del Fuego, Argentina

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Abstract. An abundant and diverse fungal assemblage was recovered from the Cullen Formation suggesting humid paleoenvironmental conditions. Thirty one different forms of fungal fruiting bodies, mostly belonging to the Microthyriales (Ascomycota), were recognized. Nineteen were assigned to fossil genera, including 6 known species. The others are presented as twelve different Types, and possibly represent new morphogenera. The genera/species *Plochmopeltinites cooksonia* Ramanujan and Rao, *Microthyriella diporata* Rao and Ramanujan, *Microthyrites, Phragmothyrites eocaenicus* Edwards, *P. kiandrensis* Selkirk and *Perisporiacites* are recorded for the first time in Argentina, enlarging their palaeogeographical distribution. A Miocene age is proposed for this formation in coincidence with that suggested for the fungal spore content and other palynological data.

Resumen. Cuerpos fructíferos fúngicos de la Formación Cullen (Mioceno) en Tierra del Fuego, Argentina. Se estudia una abundante y diversa micoflora de la Formación Cullen que sugiere condiciones paleoambientales de elevada humedad. Se reconocieron 31 diferentes cuerpos de fructificación, la mayoría perteneciente a los Microthyriales (Ascomycota). Diecinueve de ellos fueron asignados a géneros fósiles incluyendo 6 especies conocidas. Los restantes se describen como Tipos, y posiblemente representen nuevos morfogéneros. Los géneros/especies *Plochmopeltinites cooksonia* Ramanujan y Rao, *Microthyriella diporata* Rao y Ramanujan, *Microthyrites, Phragmothyrites eocaenicus* Edwards, *P. kiandrensis* Selkirk y *Perisporiacites* se registran por primera vez en Argentina, ampliando su distribución paleogeográfica. Se propone una edad miocena para esta formación en coincidencia con la sugerida por el contenido de esporas fúngicas y por la evidencia de otros datos palinológicos.

Key words. Fungal fruiting bodies. Microthyriales. Miocene. Tierra del Fuego. Argentina.

Palabras clave. Cuerpos fructíferos fúngicos. Microthyriales. Mioceno. Tierra del Fuego. Argentina.

Introduction

Fruiting bodies, particularly the Microthyriales, are some of the best known fungal remains throughout the geological record (Dilcher, 1965; Elsik, 1968). Assignment to extant genera and species has been based on morphological features, and the fact that many have been found "*in situ*" associated with leaf surfaces, stems and flowers of higher plants (Elsik, 1992).

In spite of the preliminary nature of the palaeomycological studies carried out in Argentina, some papers describing fruiting bodies of Microthyriales suggest their potential as palaeoenviromental mark-

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ers (Martínez, 1968; Durango de Cabrera and Rodríguez de Sarmiento, 1995; Romero and Castro, 1986). In the Cullen Formation, spores and other fungal remains, together with fruiting bodies, have been noted in the literature, but these generally lack morphological descriptions and/or illustrations (Vergel and Durango de Cabrera, 1988; Durango de Cabrera and Vergel, 1989; Zamaloa, 1999, 2000; Zetter *et al.*, 1999; García–Massini *et al.*, 1999). Recently, more detailed information about the Cullen Formation mycoflora has been provided by García–Massini (2001).

In this paper, we report the presence of abundant and diverse fruiting bodies recovered from the Cullen Formation. Most of them conform to Microthyriales (Ascomycetes) and others are of unknown affinity.

The Cullen Formation is part of the Austral Basin and crops out along the Atlantic coast in the northeast of Isla Grande de Tierra del Fuego in southern Argentina (Codignotto and Malumián, 1981). The outcrops extend from near Punta Catalina to 2 km south of the Tapera Sur Dell (figure 1).

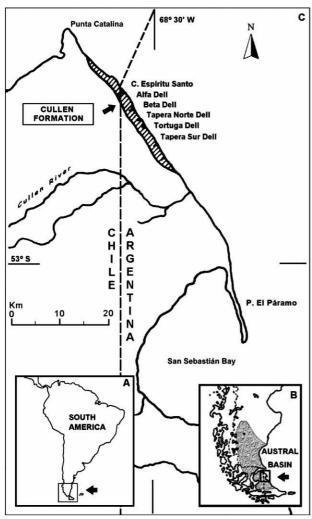


Figure 1. Location map. B) Austral Basin distribution, C) Cullen Formation outcrop, Northeast of Tierra del Fuego / Mapa de ubicación. B) Ubicación de la Cuenca Austral, C) Afloramientos de Formación Cullen, Noreste de Tierra del Fuego.

Materials and methods

Three palynological sections taken from the Cullen Formation by Zamaloa (1999) have been examined for the presence of fungal fruiting bodies. Standard palynological techniques were used to process the samples (Traverse, 1988). Slides examined are housed in the Laboratorio de Paleobotánica, Departamento de Ecología, Genética y Evolución, Universidad de Buenos Aires, Argentina, as BAFCB p.m. The coordinates given are those from the microscope Dialux 20 N° 967412 in that department.

For the classification and identification of the fungal material, we have followed Elsik (1992) and Kalgutkar and Jansonius (2001). Primary diagnostic characters used include: 1) Presence or absence of radiate symmetry, 2) Presence or absence of an ostiole, 3) Nature of the margin of the ascoma, 4) Character of the cells composing the ascoma, 5) Other special features such as porate cells. Descriptions were based on the terminology of Elsik *et al.* (1983).

Results

Of the three studied sections from the Cullen Formation, 23 stratigraphic levels yielded fungal remains. More than 500 different forms were recognized. Those samples that contain the best preserved and abundant spores also contain a large number of fruiting bodies. The forms described and/or illustrated in this contribution were selected because of their excellent preservation and/or similarity to modern fungi. None of the fruiting bodies were found in association with mycelia, spores, or attached to the leaf cuticles of any recognizable plant. Some form genera and species could be assigned to modern taxa based on information provided in the current literature (Dilcher, 1965; Romero and Castro, 1986; Durango de Cabrera and Rodriguez de Sarmiento, 1995; among others). Nineteen different forms of fruiting bodies could be accommodated within 9 known form genera, including 6 known form species, 12 forms could not be unequivocally assigned to any known taxa and are described as Types.

Systematic paleontology

Selected fruiting bodies identified in the present study are listed in Table 1. In addition, for the Types we have assigned a number only reflecting a sequential ordering, and these are presented below qualified by a brief description.

> Type I (aff. *Arnaudiella "andina*" Butin and Peredo 1986) Figure 3.G

Description. Circular fruiting body formed of a single layer of elongate–lobulate cells; more than one layer in its central portion. Cells radially arranged. Circular ostiole present in a raised central position, surrounded by a ring of thick–walled cells. The margin is lobulate. Overall size is 119 μ m, ostiole 9.1 μ m in diameter.

Comments. This specimen has most of the morphological features found in the extant *Arnaudiella "andina"* (Ascomycota, Microthyriaceae), a common parasitic fungus of the Podocarpaceae of the Chilean Andean region (Butin and Peredo, 1986).

Studied material. BAFCB p.m. 240, 48.8/111.6.

Type II (aff. *Arnaudiella "andina"* Butin and Peredo 1986) Figure 3.H

Description. Polygonal fruiting body, formed by one layer of elongated cells. Two layers appear to develop toward the central part of the body. The body has 2 approximately circular slightly raised ostioles. Around each ostiole the cell wall is markedly thicker forming circular rings. The cells are approximately

Table 1. List of taxa of fungal fruiting bodies recognized in the Cullen Formation. Those marked with * are recorded for the first time in Argentina / Lista de taxones de cuerpos fructíferos reconocidos en la Formación Cullen. Los indicados con * son citados por primera vez en Argentina.

Micropeltaceae	
* Plochmopeltinites cooksonia Ramanujam & Rao 1973	Figure 2.A
Plochmopeltinites masonii Cookson 1947	Figure 2.B-E
* Plochmopeltinites sp. 1	Figure 2.F
* Plochmopeltinites sp. 2	Figure 2.G
* Plochmopeltinites sp. 3	Figure 2.H
* Plochmopeltinites sp. 4	Figure 2.I
Microthyriaceae	rigure 2.1
Asterothyrites (Cookson) Kalgutkar &	
Jansonius 2001	Figure 2.J
	_
Callimothallus persutus Dilcher 1965	Figure . 2. K
* Callimothallus sp.	Figure 2.L
* Microthyriella diporata Rao & Ramanujam 1976	Figure 2.M
* Microthyrites sp.	Figure 2.N
* Phragmothyrites eocaenicus Edwards 1922	Figure 2.O-G
* Phragmothyrites kiandrensis Selkirk 1975	Figure 3.A
* Phragmothyrites sp.	Figure 3.B
Perisporiaceae	
•	Figure 3.C
	O
	Figure 3.F
	O
v	Figure 3. D
Incertae sedis	0
* Types I to XII	Figure 3.G-S
Perisporiaceae * Perisporiacites sp. Trichopeltaceae Trichopeltinites sp. Trichothyriaceae * Trichothyrites sp. 1 * Trichothyrites sp. 2 Incertae sedis	Figure 3.C Figure 3.F Figure 3. D Figure 3.E

radially arranged. The margin is slightly lobulate to fimbriate. Size 110.5 x 100.5 $\mu m,$ ostioles 11 and 14 $\mu m.$

Comments. The shape and spatial arrangement of cells in this specimen resembles Type I, only differing in the number of ostioles.

Studied material. BAFCB p.m. 213, 38.7/104.5.

Type III Figures 3.I, J

Description. Fruiting body with an irregular to quadrangular shape, and formed of one to two layers of large lobulate, thin-walled, radially arranged cells. The body shows a large pseudo–ostiole of irregular to near circular outline. The margin is lobulate. Size 67 x 59 μ m, 35 x 29 μ m, pseudo–ostiole 14 to 16 μ m, 5 to 9 μ m. **Comments.** The main feature of this type is that the cells, considered individually, resemble those designated as "germlings of Microthyriaceae" by Dilcher (1965).

Studied material. BAFCB p.m. 240, 43.8/101.3, 44.1/102.

Type IV ("Parabrefeldiellites" Elsik 1992) Figure 3.K

Description. Flattened fruiting body of polygonal outline with 7 sides. Body formed of one layer of cells, aparently two layers occur in the central part of the body. Cells rectangular to quadrangular, with thick walls, and arranged in parallel rows that deve-

lop in four directions. Margin smooth and entire. Astomate body. Size $85 \times 59 \mu m$.

Comments. This specimen is closely similar to the informal genus "*Parabrefeldiellites*" Elsik 1992, previously reported from sediments of Miocene to Recent age (Elsik, 1992).

Studied material. BAFCB p.m. 193, 40.8/100.

Type V Figure 3.L

Description. This specimen is represented by approximately half of a spherical body, and formed by thin–walled, rectangular to circular cells. Extending from the convex part of the body are septate processes, 3 to 5 cells long. These processes have a slightly pyramidal shape and blunt apex. Diameter of the body 40 μm; length of processes 25 to 30 μm cell wall thickness 1 to 2 μm.

Comments. According to its shape and cell arrangement, this fruiting body looks similar to *Appendicisporonites* Saxena and Khare 1992, but differs in the presence of septa in the processes that arise from the central body. The named genus was originally described as dispersed spores from the Tertiary of India (Saxena and Khare, 1992) but later suggested as a fruiting body either of Microthyriaceae or Coelomycetes (Kalgutkar and Jansonius, 2001).

Studied material. BAFCB p.m. 240, 30.6/99.

Type VI Figure 3.M

Description. Circular fruiting body of, at least, two layers of cells of irregular shape, arranged in approximately radial pattern. Four zones are distinguishable constituting triangular sectors of a circle; cells inside are heavily pigmented. A pseudo–ostiole of irregular shape is in the center of the body. The margin is lobulate to irregular. Diameter of the body 58.5 μm, pseudo–ostiole 9 μm.

Studied material. BAFCB p.m. 240, 44/98.

Type VII Figure 3.N

Description. Circular fruiting body constructed of one to two (centrally located) layers of cells, of a roughly polygonal shape. Cell walls located in the periphery of the body are less thick compared to those of the more centrally located cells. Astomate body. The cells are radially arranged. Margin is not continuous but formed by the wall projections of the peripheral cells. Diameter of the body 87 μ m; thickness of the cell walls 1 to 2 μ m.

Studied material. BAFCB p.m. 249, 32.8/112.8.

Type VIII Figure 3.O **Description.** Circular to elongate fruiting body constructed of a layer of elongate and lobulate cells; this feature is evident at the periphery. The cells are radially arranged and a large ostiole of irregular contour is distinguished. The margin is lobulate. Diameter of the body 115 μ m, ostiole 20 μ m.

Studied material. BAFCB p.m. 240, 26.5/98.8.

Type IX Figure 3.P

Description. Circular fruiting body, constructed of semicircular to ovoid cells, arranged in a radial pattern. The cell walls are thin and no ostiole is distinguished. The margin appears irregular because the cells in the periphery are not intact. Diameter of the body 59 μ m.

Studied material. BAFCB p.m. 249, 39.9/102.2.

Type X Figure 3.Q

Description. Large circular fruiting body having several layers of heavily pigmented cells. Cells appear to be elongated, thick-walled and radially arranged. There is a slightly raised circular central ostiole. The margin is irregularly sinuate. Diameter 303.5 μ m; ostiole 24 μ m.

Studied material. BAFCB p.m. 235, 37.3/96.9.

Type XI Figure 3.R

Description. Fruiting body of irregular to polygonal shape. Body formed of large lobulate cells radially arranged with respect to one or two central cells. Astomate body. From most cells elongate appendages emerge perpendicularly showing a rather circular swollen head, which is curved. In some cases, more than one appendix protrudes from the same cell. The margin of the body is slightly lobulate. Size $35~\mu m$.

Studied material. BAFCB p.m. 240, 38.8/110.6.

Type XII Figure 3.S

Description. Fruiting body of quadrangular shape, formed of four central cells and eleven lobulate peripheral cells. Astomate body, lobulate margin. Central cells with differentially thickened walls of up to 2 μ m in thickness. Size 33 x 30 μ m.

Studied material. BAFCB p.m. 240, 46.6/101.9.

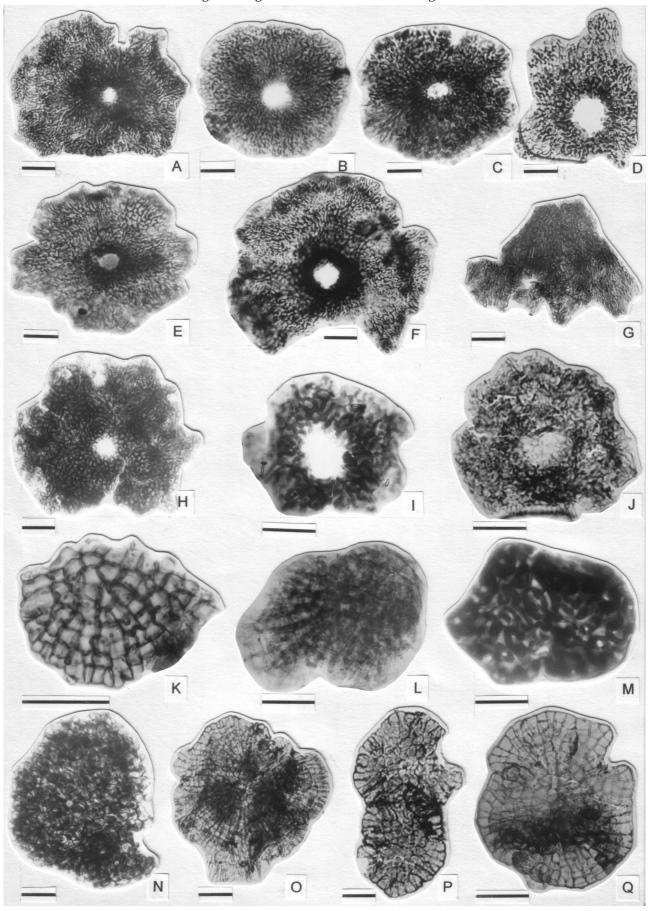
Discussion

It has been suggested that with the origin of the angiosperms a major diversification within the Ascomycetes occurred giving rise to epiphytic and saprophytic groups such as the Microthyriales (Kalgutkar and Jansonius, 2001). Elsik (1978, 1992) hypothesized that from the Early Cretaceous on Microthyriales and Angiosperms coexisted in the same habitats promoting a continuous enrichment of the community and creating additional microhabitats occupied by other fungi. As a consequence, it is not unusual to find a high diversity of fossil fungi associated to the presence of angiosperms in sediments spanning the Cretaceous, Paleogene and Neogene. The Cullen Formation is a representative example of such situation.

The sediments studied here contain numerous morphologically diverse fungal fruiting bodies. Based on the affinities with known extant and fossil forms, some ideas may be presented regarding previously suggested palaeoenvironmental conditions at the time of deposition (Zamaloa, 1999, 2000). Other specimens found in this formation could not be assigned to extant taxa or known fossil forms; however, some of these display characteristic morphological features, which facilitate their identification and may be useful as palaeoenvironmental and/or perhaps stratigraphic markers in future works. Particularly, the specimens designated as Types I and II result similar to extant Arnaudiella "andina" (Ascomycota, Microthyriaceae), a common parasitic fungus of the Chilean Andean region (Butin and Peredo, 1986).

During the time of deposition of the sediments comprising the Cullen Formation, it is postulated that a temperate humid forest, mostly composed of angiosperms of the Nothofagaceae and gymnosperms of the Podocarpaceae and Araucariaceae, formed the environment where an abundant mycoflora developed. Among angiosperms, representatives of about 30 different families were recorded. These include Apiaceae, Asteraceae, Chenopodiaceae, Cunoniaceae, Cyperaceae, Gunneraceae, Malvaceae, Menyanthaceae, Myrtaceae, Onagraceae, Poaceae, Proteaceae, Rosaceae, Rubiaceae, Sapindaceae, Sparganiaceae/Typhaceae and Winteraceae. A

Figure 2. Fossil fungal fruiting bodies from the Cullen Formation. Graphic scale = 20 μm /Cuerpos fructiferos fúngicos de la Formación Cullen. Escala gráfica = 20 μm. **A, Plochmopeltinites cooksonia** Ramanujan & Rao BAFCB p.m. 240: 39.7/103.4; **B-E, Plochmopeltinites masonii** Cookson, **B,** BAFCB p.m. 210: 43.5/109.4; **C,** BAFCB p.m. 240: 46.7/108.1; **D,** BAFCB p.m. 240: 37.3/95; **E,** BAFCB p.m. 252: 31.6/97.2; **F, Plochmopeltinites** sp. 1 BAFCB p.m. 235: 31.7/93.2; **G,** Plochmopeltinites sp. 2 BAFCB p.m. 240: 38/103; **H,** Plochmopetinites sp. 3 BAFCB p.m. 240: 46.3/103.2; **I,** Plochmopetinites sp. 4 BAFCB p.m. 210: 29.6/91.7; **J,** Asterothyrites sp. BAFCB p.m. 210: 42.6/92.6; **K,** Callimothallus persutus Dilcher BAFCB p.m. 242: 47.1/102.4; **L,** Callimothallus sp. BAFCB p.m. 240: 48.7/110.7; **M,** Microthyriella diporata Rao & Ramanujan BAFCB p.m. 193: 39.5/105.7; **N,** Microthyrites sp. BAFCB p.m. 240: 27/98; **O-Q,** Phragmothyrites eocaenicus Edwards, **O,** BAFCB p.m. 240: 32.4/98.5; **P,** BAFCB p.m. 240: 35.3/99; **Q,** BAFCB p.m. 227: 50.5/95.1.



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diverse flora of bryophytes and pteridophytes was also documented (Zamaloa, 2000). It is suggested that these bioclimatic conditions promoted the large fungal diversity found in this formation. Additionally, taphonomic conditions, particularly the high rate of sedimentation, in part, as a consequence of the periodic overflow of the meandriform rivers, created an anoxygenic microenvironment that enabled the excellent preservation of many of the fungal remains.

Most of the recovered fruiting bodies are members of the Ascomycota representing the families Micropeltaceae (*Plochmopeltinites cooksonia, P. masonii, Plochmopeltinites* sp. 1, *Plochmopeltinites* sp. 2, *Plochmopeltinites* sp. 3, *Plochmopeltinites* sp. 4), Microthyriaceae (*Asterothyrites* sp., *Callimothallus persutus, Callimothallus* sp., *Microthyriella diporata, Microthyrites* sp., *Phragmotyrites eocaenicus, P. kiandrensis, Phragmothyrites* sp.), Trichopeltaceae (*Trichopeltinites* sp.), Trichothyriaceae (*Trichothyrites* sp. 1, *Trichothyrites* sp. 2), and Perisporiaceae (*Perisporiacites* sp.), the first four families belonging to the Microthyriales and the Perisporiaceae belonging to the Dothidiales (Tiffney and Barghoorn, 1974; Kalgutkar and Jansonius, 2001).

Dilcher (1965) described fruiting bodies of *Callimothallus* and *Microthyriella* from the Eocene of Tennessee epiphytically associated to cuticles of Sapindaceae and Rosaceae. These latter angiosperm families were also part of the flora of the Cullen Formation and pollen grains with these affinities were found in stratigraphic levels coincident with those where fruiting bodies of *Callimothallus* and *Microthyriella* were found, further establishing a positive correlation between both observations.

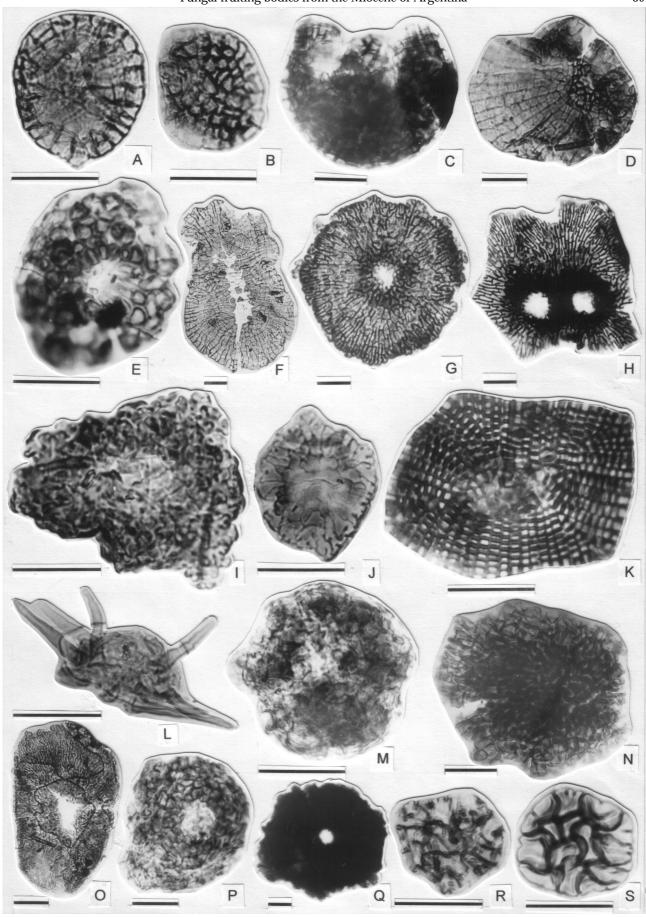
Several authors have pointed out the value of Microthyriaceous fungi as indicators of moist and humid climates and/or subtropical temperatures (Dilcher, 1965; Lange, 1976; Kalgutkar and Jansonius, 2001). Cookson (1947) suggested that the Microthyriaceae are more abundant in regions of warm temperate climates characterised by a high relative ambient moisture. Moreover, Elsik (1992) noted that the single most important external factor responsible for their distribution was not temperature, but rather the mean rainfall, and that this feature provided a positive correlation between their presence

and rainfall values higher than 1000 mm/year. As an example, *Trichothyrites* was found in humid zones of high temperature (Cookson, 1947) and in temperate, non-tropical and high precipitation regions (Rosendahl, 1943), showing once more that their presence was more dependent on the availability of humid conditions rather than on the temperature. Finally, the presence of these fungi in conjunction with spores and pollen belonging to water demanding taxa (Zamaloa, 2000) reinforces the hypothesis of prevailing humid climate conditions at the time of deposition of the sediments of the Cullen Formation.

Many of the fruiting bodies described and illustrated here (i.e. *Plochmopeltinites cooksonia*, *P. masonii*, *Callimothallus persutus*, *Microthyriella diporata*, *Phragmothyrites eocenicus*, *P. kiandrensis*, "*Parabrefeldiellites*", *Appendicisporonites*) are similar to those found in other basins (Cookson, 1947; Dilcher, 1965; Edwards, 1922; Elsik, 1992; Ramanujam and Rao, 1973; Rao and Ramanujam, 1976; Saxena and Khare, 1992; Selkirk, 1975). Some of these forms are cited for the first time for Argentina (Table 1) thus enlarging their palaeogeographical and/or stratigraphic distribution.

The presence of some selected taxa allows us to hypothesize on the age of the Cullen Formation. Phragmothyrites kiandrensis (Early Miocene), Plochmopeltinites masonii (Oligocene to Miocene), Plochmopeltinites cooksonia (Miocene), Microthyriella diporata (Miocene) (age ranges taken from Kalgutkar and Jansonius, 2001) and "Parabrefeldiellites" (Miocene to Recent) (Elsik, 1992) indicate a Miocene age. Additionally, the presence of fungal spores referred to Dyadosporites bhardwaji (Varma and Rawat) Kalgutkar and Jansonius 2001 (Eocene to Miocene), D. cannanorensis Ramanujan and Rao 1978 (Miocene), Pucciniasporites arcotensis Ramanujan and Ramachar 1980 (Miocene) and Frasnacritetrus siwalikus Saxena, Singh and Rao 1987 (Miocene to Pliocene) (age ranges taken from Kalgutkar and Jansonius, 2001) in the Cullen Formation assemblage supports a Miocene age. This age is coincident with that obtained by analyzing the overall pollen/spore contents (Zamaloa, 2000). According to these results, this is the first record of Perisporiacites, Callimothallus persutus and Phragmothyrites eocaenicus in sediments younger than Eocene.

Figure 3. Fossil fungal fruiting bodies from the Cullen Formation. Graphic scale = 20 μm / *Cuerpos fructíferos fúngicos de la Formación Cullen. Escal gráfica* = 20 μm. **A, Phragmothyrites kiandrensis** Selkirk BAFCB p.m. 240: 37.9/99.1; **B, Phragmothyrites** sp. BAFCB p.m. 240: 38.1/110.1; **C, Perisporiacites** sp. BAFCB p.m. 240: 31.2/104.8; **D, Trichothyrites** sp. 1 BAFCB p.m. 187: 32.1/92.2; **E, Trichothyrites** sp. 2 BAFCB p.m. 240: 47.6/101; **F, Trichopeltinites** sp. BAFCB p.m. 235: 36.7/100.5; **G,** Type I (aff. *Arnaudiella "andina*" Butin & Peredo) BAFCB p.m. 240: 48.8/111.6; **H,** Type II (aff. *Arnaudiella "andina*" Butin & Peredo) BAFCB p.m. 213: 38.7/104.5; **I-J,** Type III, I BAFCB p.m. 240: 43.8/101.3; **J,** BAFCB p.m. 240: 44.1/102; **K,** Type IV ("*Parabrefeldiellites*" Elsik) BAFCB p.m. 193: 40.8/100; **L,** Type V BAFCB p.m. 240: 30.6/99; **M,** Type VI BAFCB p.m. 240: 44/98; **N,** Type VII BAFCB p.m. 249: 32.8/112.8; **O,** Type VIII BAFCB p.m. 240: 26.5/98.8; **P,** Type IX BAFCB p.m. 249: 39.8/102.2; **Q,** Type X BAFCB p.m. 235: 37.3/96.9; **R,** Type XI BAFCB p.m. 240: 38.8/110.6; **S,** Type XII BAFCB p.m. 240: 46.6/101.9.



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Conclusions

The Cullen Formation sediments have yielded a great diversity of fungal fruiting bodies, which are abundant in several samples. Of the hundreds of specimens observed, 31 different forms are presented in this contribution. Of these, 19 were assigned to known fossil genera, including 6 known fossil species. The others correspond to 12 different Types and possibly represent new morphogenera.

The genera and/or species *Plochmopeltinites cooksonia*, *Microthyriella diporata*, *Microthyrites*, *Phragmothyrites eocaenicus*, *P. kiandrensis* and *Perisporiacites* are recorded for the first time in Argentina, thus enlarging their palaeogeographical distribution. The genera and/or species *Perisporiacites*, *Callimothallus persutus* and *Phragmothyrites eocaenicus* are recorded for the first time in sediments younger than Eocene. A positive correlation appears to exist between the diversity of fungal fruiting bodies and the diversity of spores and pollen, especially to that of angiosperm source.

The fungal palaeoflora flourished under rather humid climate conditions. A Miocene age is proposed for this formation coinciding with that suggested for the fungal spore content, as well as other palynological data.

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