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Glomeromycota in mosses: arbuscular mycorrhizal structures in *Leptodontium capituligerum* (Pottiaceae) from the Argentine Chaco Serrano

Glomeromycota en musgos: estructuras micorrícicas arbusculares en *Leptodontium capituligerum* (Pottiaceae) del Chaco Serrano argentino

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Summary: Arbuscular mycorrhizal fungi (AMF) associations in mosses remain poorly documented compared with those reported for liverworts and hornworts. In this contribution, we report fungal structures compatible with Glomeromycota in living gametophytes of *Leptodontium capituligerum* (Pottiaceae) from the Chaco Serrano of Tucumán, Argentina. Gametophytes were clarified with KOH, stained with trypan blue, and examined using light and scanning electron microscopy. Intercellular aseptate hyphae, intracellular hyphal coils, arbuscules, vesicles, and spores morphologically compatible with AMF were observed in leaves and stems. Both *Arum*- and *Paris*-type morphologies were detected. In addition, dark septate endophytes and other septate fungi were associated with leaves and rhizoids. These observations provide additional evidence supporting fungal symbioses in mosses and reinforce the hypothesis that associations between Bryophyta and Glomeromycota may be more frequent than previously assumed.

Key words: Arbuscular mycorrhizal fungi, Bryophyta, Glomeromycota, mosses, Pottiaceae, symbiosis.

Resumen: Las asociaciones entre hongos micorrícicos arbusculares (HMA) y musgos están escasamente documentadas en comparación con las registradas para otros grupos de briófitas. El objetivo de este trabajo es describir estructuras fúngicas compatibles con Glomeromycota en gametófitos vivos de *Leptodontium capituligerum* (Pottiaceae) provenientes del Chaco Serrano de Tucumán, Argentina. Los gametófitos se aclararon con KOH, se tiñeron con azul de tripano y se examinaron mediante microscopía óptica y electrónica de barrido. En hojas y tallos se observaron hifas aseptadas intercelulares, ovillos hifales intracelulares, arbúsculos, vesículas y esporas morfológicamente compatibles con HMA. Se detectaron patrones de colonización de tipo *Arum* y *Paris*. Adicionalmente, se registraron endófitos septados oscuros y otros hongos septados asociados con hojas y rizoides. Estos hallazgos aportan evidencia sobre la presencia de simbiosis fúngicas complejas en Bryophyta y refuerzan la hipótesis de que las asociaciones con Glomeromycota son más frecuentes de lo asumido tradicionalmente en musgos.

Palabras clave: Bryophyta, Glomeromycota, hongos micorrícicos arbusculares, musgos, Pottiaceae, simbiosis.

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Introduction

Bryophytes comprise the three major lineages of land plants: mosses (Bryophyta), liverworts (Marchantiophyta), and hornworts (Anthocerotophyta). While associations with arbuscular mycorrhizal fungi (AMF; Glomeromycotina) are widely documented and considered ancestral in liverworts and hornworts (Rayner, 1927; Kelley, 1950; Gerdemann, 1968; Harley, 1969; Albornoz *et al*., 2022), their presence in mosses has remained a subject of intense debate. Historically, mosses were viewed as asymbiotic or only occasionally colonized by opportunistic fungi, primarily in senescent tissues (Read *et al*., 2000; Pressel *et al*., 2010).

In the Chaco Serrano of Tucumán (Argentina), Albornoz *et al*. (2022) confirmed the presence of AMF and dark septate endophytes (DSE) in the thalloid liverwort *Plagiochasma rupestre* (J. R. Forst. & G. Forst.) Steph., describing both *Arum*- and *Paris*-type colonization patterns. However, such evidence has been notably absent for the mosses of the region until now.

Current investigations are challenging this long-standing paradigm. Catania *et al*. (2025) reported the landmark discovery of a full set of canonical AMF structures-including arbuscules, the functional site of nutrient exchange-within living gametophytes of Pottiaceae mosses, such as *Gertrudiella uncinicoma* (Müll. Hal.) G. M. Suárez & Schiavone and *Pleurochaete luteola* (Besch.) Thér., in the Argentine Chaco Serrano.

Expanding the global context of these interactions, Kelly *et al*. (2026) identified novel Glomeromycotina-moss associations in dryland biocrusts of North America, observing intracellular branching in healthy *Trichostomopsis australasiae* (Hook. & Grev.) H. Rob. cells. Furthermore, Godoy *et al*. (2026) described spores of Glomeromycota [e.g., *Acaulospora laevis* Gerd. & Trappe, *Ambispora gerdemannii* (S. L. Rose, B.A. Daniels & Trappe) C. Walker, Vestberg & A. Schüßler] inhabiting the interior of "mossballs" formed by *Rigodium implexum* Kunze ex Schwägr. in southern Chile, suggesting that mosses may act as critical microhabitats for AMF persistence and dispersal.

Despite these advances, documentation of AMF in Bryophyta remains scarce compared to other land plant lineages. The increasing evidence of these symbioses highlights the need for further studies integrating anatomical and ecological data, particularly in xeric environments where the extremophilic mosses are vital ecosystem components.

The aim of this study is to present the first record of colonization by AMF and septate endophytes in *Leptodontium capituligerum* Müll. Hal. (Pottiaceae) from the Argentine Chaco Serrano, providing a detailed morphological description of these associations.

Materials and Methods

Plant sampling

Moss gametophyte samples were collected from several sites in the Chaco Serrano forest of Tucumán, Argentina. This mountain transitional zone between the Yungas and the arid Chaco ecoregions is characterized by mountains and valleys with vegetation adapted to xeric and semi-dry environments. The specimens were examined using traditional techniques for Pottiaceae, including the analysis of internal leaf and stem anatomy and color reactions to KOH solution. Taxonomic identification of species followed protocols by Zander (1972, 1993). Vouchers are deposited in the Fundación Miguel Lillo Herbarium (LIL).

AMF prospection and staining

Living gametophytes of *L. capituligerum* were collected from the study site, washed with tap water, and preserved in 70% ethanol at room temperature. Samples were clarified in 10% potassium hydroxide (KOH) at room temperature for 10 to 15 days, followed by acidification with 1% hydrochloric acid (HCl) for 10 minutes. Tissues were then stained with 0.05% trypan blue in glycerin (Cottet *et al.*, 2018).

Microscopic analysis

Characteristic AMF structures were examined using a stereomicroscope (Olympus SZX7, Tokyo, Japan) and an optical microscope (Axiostar Plus, Zeiss, Göttingen, Germany). For ultrastructural details, samples were studied using scanning electron microscopy (SEM,

Supra 55VP, Zeiss, Oberkochen, Germany). These specimens were fixed in Karnovsky solution, critical-point dried, and coated with gold-palladium. Colonization types were classified following Dickson (2004) based on the presence of inter- and intracellular hyphae, arbuscules, and hyphal coils. AMF spores were identified according to morphological criteria established by Schenck and Pérez (1990) and Schüßler *et al*. (2001).

Material examined: **ARGENTINA**. **Tucumán**: Dep. Trancas, San Pedro de Colalao, 26°15'31''S, 65°32'18''W, 02-XII-2022, *G. Suárez 1911* (LIL).

Results

The plants of *L. capituligerum* were found forming mats, greenish- to yellowish-brown. Stems erect. Leaves ovate-lanceolate to lanceolate, with recurved margins in the lower part and serrate to dentate margins in the upper 1/3; apex acute to broadly acute; keeled above, with a sheathing, decurrent base.

Microscopic examination of living gametophytes revealed abundant fungal structures morphologically compatible with arbuscular mycorrhizal fungi. Intercellular aseptate hyphae, hyphae occupying the host cell lumen (rather than the host protoplast), intracellular hyphal coils, arbuscules, vesicles, and spores were observed in leaves and stems (Fig. 1).

The colonization pattern corresponded to both *Arum*- and *Paris*-type morphologies. *Arum*-type morphology was characterized by thin and thick hyphae arranged parallel to the gametophyte surface, forming characteristic "H"-shaped configurations (Fig. 1A, B). *Paris*-type morphology was represented by intracellular hyphal coils (Fig. 1G, H).

Arbuscules associated with aseptate hyphae were observed within gametophytic tissues (Fig. 1C, D, F). Vesicles were ellipsoidal, globose-subglobose, or elongated and connected to hyphae. Spores morphologically compatible with *Glomus* sp. were also detected (Fig. 1I, J).

In addition to AMF structures, dark septate endophytes (DSE) and unknown septate fungi (USH) were observed (Fig. 1K, L). Dark septate endophytes occurred mainly in leaves, whereas unknown septate fungi were associated with rhizoids.

Discussion

The discovery of arbuscular mycorrhizal fungi (AMF) structures in *L. capituligerum* provides additional evidence for the presence of complex fungal symbioses in mosses. Historically, these associations were considered rare or restricted to specific lineages like *Takakia* S. Hatt. & Inoue (Read *et al*., 2000; Pressel *et al*., 2010). However, the results presented here align with a growing body of evidence suggesting that mosses, particularly those in the Pottiaceae family, are capable of forming functional symbioses with Glomeromycota.

In the Chaco Serrano of Argentina, Albornoz *et al*. (2022) established a regional precedent by documenting AMF in the thalloid liverwort *P. rupestre*. While liverworts have a well-known history of such associations, our findings extend this knowledge to the Bryophyta (mosses) of the same region. This is particularly relevant when compared to the recent landmark study by Catania *et al*. (2025), who reported the first full set of diagnostic AMF structures in other Pottiaceae species like *G. uncinicoma* and *P. luteola* in the Argentine Chaco. The presence of arbuscules in *L. capituligerum* reinforces the idea that these structures are not mere chance colonizations but putative exchange sites within living gametophytes.

From a global perspective, our observations are consistent with the findings of Kelly *et al*. (2026) in North American dryland biocrusts, where *T. australasiae* (another Pottiaceae) showed intracellular branching. The occurrence of both *Arum*- and *Paris*-type colonization in *L. capituligerum* suggests a high degree of plasticity in the interaction, possibly as an adaptation to the fluctuating environmental conditions of the Chaco Serrano. Furthermore, the detection of *Glomus* sp. spores within the gametophyte tissues

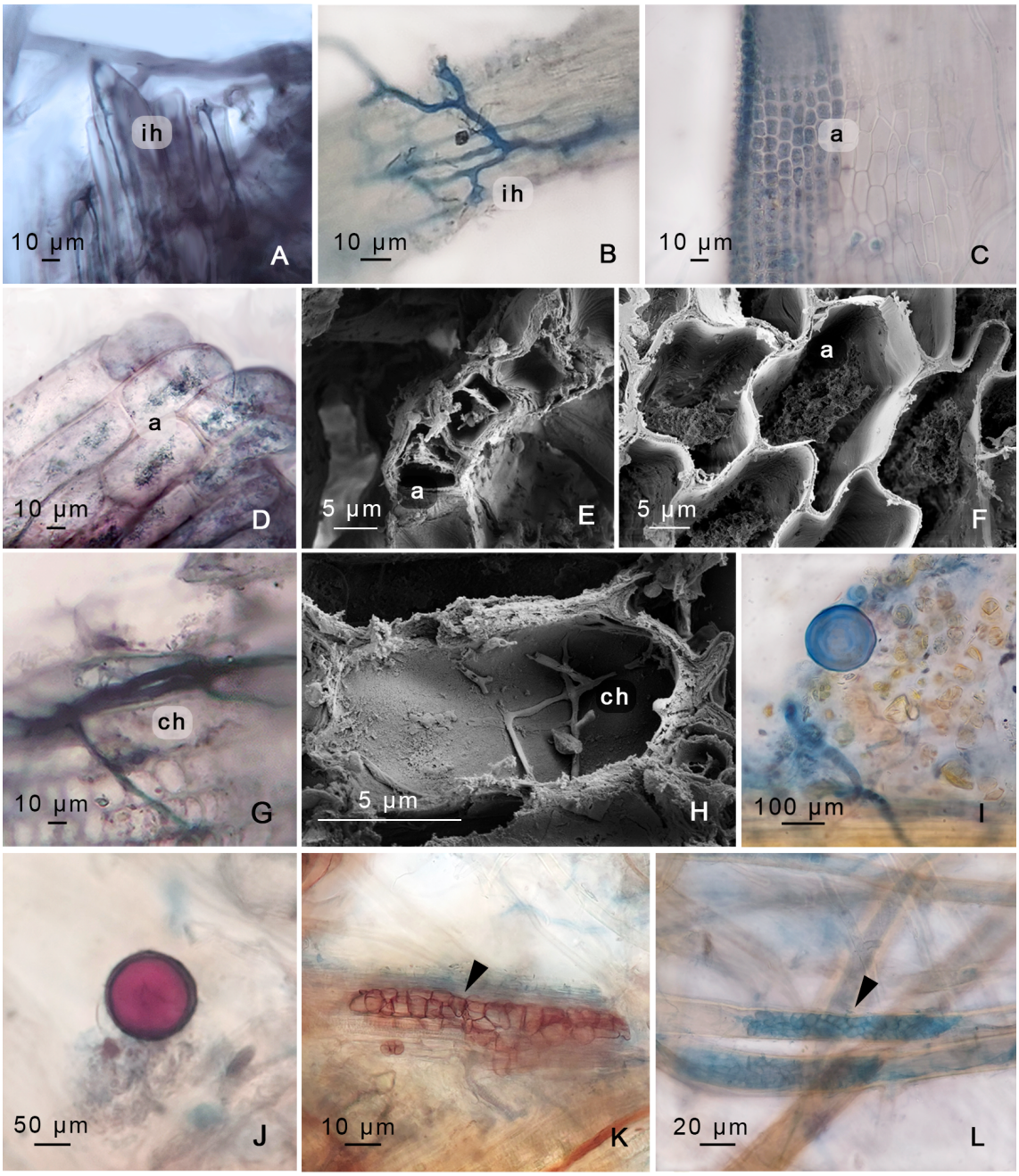

Fig. 1. *Leptodontium capituligerum*. Colonization by Arbuscular Mycorrhizal Fungi. A-B: Intercellular hyphae (IH). C-F: Arbuscules (a). C-E: In leaf. F: In stem. G-H: Coil hyphae (ch). I-J: Spore of *Glomus* sp. K: Septate endophyte, microsclerotia (arrowed). L: Unknown septate fungus (arrowed). A-D, G, I-L, Light micrographs. E-F, H, Scanning electron micrographs. A-L, *Suárez 1911* (LIL).

echoes the work of Godoy *et al*. (2026) in Chile, who proposed that mosses could serve as critical microhabitats for the persistence and co-dispersal of Glomeromycota spores.

The co-occurrence of AMF with dark septate endophytes (DSE) and other septate fungi in *L. capituligerum* highlights the complexity of the moss mycobiome. As

suggested by Lavado and Chiocchio (2025), these multi-species fungal associations may act as a combined tool for plant survival in sustainable and stressed environments. In xeric habitats like the Chaco Serrano, these symbioses likely play a crucial role in nutrient uptake and water stress tolerance, challenging the traditional view of mosses as independent organisms.

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Author Contributions

LIJ, MVC, PLA and GMS conceived the study. LIJ, MVC and PLA performed laboratory analyses and microscopy. GMS identified the Bryophyta material and curated voucher specimens. All authors contributed to data interpretation, manuscript writing and revision, and approved the final version of the manuscript.

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